Chapter 10

General Biology of Major Prey Species of the California Spotted Owl

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Full understanding of the habitat relations of California spotted owls depends, in part, on knowledge of the habitat relations of their primary prey species. For example, the northern flying squirrel is the primary prey of the owl in conifer forests of the Sierra Nevada, comprising as much as 61 to 77 percent of the total biomass eaten in some localities and seasons (table 4A). The dusky-footed woodrat is the primary prey in lower-elevation forests and woodlands of the Sierra Nevada and throughout all habitats in southern California, making up 74-94 percent of the diet, by weight, in various areas. Current evidence indicates that suitable nest sites and the most common foods of northern flying squirrels are usually found together in mature and older forests, which may help us understand why spotted owls forage more often in such forests. Woodrats are typically associated with shrubfields, especially those dominated by thick-leaved, evergreen species. Spotted owls in the Sierran foothills and in southern California commonly occur in forests and woodlands with a light to moderate shrub understory, or that adjoin more extensive stands of chaparral. In addition, radio-tracking studies of spotted owls in the Sierra NF have shown that their home ranges in Sierran mixed-conifer forests are measured in thousands of acres, but those in foothill riparian/hardwoods are measured in hundreds of acres (Neal et al. 1990). This difference is probably related, at least in part, to the facts (1) that woodrat densities are generally several times higher than flying squirrel densities and (2) that woodrats weigh nearly twice as much as flying squirrels.

Here, to expand a general understanding of spotted owl ecology, we present brief biological descriptions of several species of small to mid-sized mammals that most commonly occur in diets of the California spotted owl (see Chapter 4).

Dusky-Footed Woodrat

Distribution and Habitat

Dusky-footed woodrats occur in the Pacific Coast region from the Oregon side of the Columbia River to northern Baja California. Within the range of the California spotted owl, they inhabit coastal, piedmont, and montane chaparral and forest communities. Evergreen or live oaks and other thick-leaved shrubs are important habitat components throughout this woodrat's geographic range (see color photo 5-29). They are most numerous where shrub cover is dense, and least abundant in open areas (Fitch 1947). They are one of few small mammal species of chaparral habitats that flourish in old, dense stands (Quinn 1990).

Habitats that are unsuited or poorly suited for dusky-footed woodrats include open grasslands or fallow, weedy ground; sparsely wooded forests; woodlands solely of conifers or with little shrub understory; and pure stands of chamise, manzanita, or ceanothus (Linsdale and Tevis 1951).

In the Sierra Nevada, this woodrat occurs generally below 5,000 feet in elevation (lower in the north-about 3,300 feet at Mt. Lassen and 4,000 feet in Yosemite National Park (NP), and higher to the south-rare at 6,000-6,500 feet in the Kern River drainage). It occupies foothill riparian/hardwoods in the northern San Joaquin Valley. The highest capture rates of woodrats in the foothills of the west-central Sierra Nevada were in chaparral, woodland, and forest communities with a mix of overstory trees and shrubs (table 10A). These results appear to agree with those of Sakai and Noon (1992a), who indicate that dusky-footed woodrats in northwestern California are most abundant in brushy stands of sapling/early-aged poletimber. In the southern Sierra Nevada (Kern County), in a chaparral community of ceanothus and interior live oak between 2,560 and 3,200 feet in elevation, woodrats were most often trapped around patches of rock gooseberries, and their nests were common where gooseberry thickets encircled rock outcrops or dead snags (Lawrence 1966).

In the San Bernardino Mountains, the dusky-footed woodrat occurs on both the Pacific and desert slopes, ranging from about 1,600 feet on the Pacific slope and 3,800 feet on the desert slope up to at least 8,000 feet on both sides, where it is the primary prey species of the spotted owl (LaHaye pers. comm.). Grinnell (1908) found most nests in California scrub oak and pinyon associations and few along willow-lined canyons. They occur in big sagebrush/pinyon-juniper woodlands in the New York-Providence mountain chain in eastern San Bernardino County.

In the San Gabriel Mountains, dusky-footed woodrats occur on both the Pacific and desert slopes, exhibiting the same elevational distribution as in the San Bernardino Mountains. In the coastal sage belt, they are restricted to areas close to intermittent streams supporting tall shrubs or small trees. Nests are built mostly of white sage in isolated clumps of lemonade sumac. Population densities -generally are low in this community (M'Closkey 1972). Higher numbers are found in adjacent canyons on densely vegetated slopes. At higher elevations on the desert side, favored spots for nests are thickets of chokecherries, mountain whitethorn, and currants. In the pinyon-juniper woodlands, both conifer species were used for nest sites; but Califor-

Table l0A-*Captures of small mammals in snap traps (Museum Specials and Victor rat traps) in various habitats and seral stages in the western Sierra Nevada, California, based on sampling in Amador, Calaveras, Mariposa, Nevada, Placer, and Tuolumne counties. Values are captures per trap night[1] (adapted from Williams and Johnson 1979).*

Habitat and Seral stage	Species captured				
	Dusky-footed woodrat	Brush mouse	California mouse	Deer mouse	Pinyon mouse
Annual grassland	0	0	0	0.0910	0
Chaparral					
Grass/forb	0	0	0	0.2340	0
Light shrub	0.0039	0.0133	0	0.0261	0.0011
Dense shrub	0.0098	0.0031	0	0.016	0.0004
Oak/digger pine					
Seral	0.0007	0	0	0.0074	0
Mature	0.0052	0.0319	0.0007	0.0059	0
Ponderosa pine					
Seral	0.0011	0.0015	0	0	0.0011
Mature	0.0007	0	0	0.0020	0
Mixed-conifer					
Seral	0.0048	0.0045	0	0.0003	0.0003
Mature	0.0030	0.0052	0	0.0015	0
Riparian/hardwood					
Low elevation	0.0044	0.0044	0	0.0022	0.0011
Mid-elevation	0	0	0	0.0007	0

[1] Data from 33 transects; total trap nights = 19,824.

nia scrub oak seemed to be preferred wherever it occurred. They sometimes build no visible nests where talus is available (Vaughan 1954), although careful examination usually reveals clipped branches adjacent to crevice or tunnel entrances (Sakai and Noon 1992a).

In central coastal areas, dusky-footed woodrats appear to prefer closed woods on drier sites, including a high percentage of live oaks with a mixed shrub understory (California coffeeberry and poison oak are the most prevalent shrubs). North-facing slopes meet these conditions best in the area around Hastings Natural History Reservation (hereafter, Hastings Reservation) at about 1,500-2,500 feet in elevation, where intermittent streams with willows also provide high-quality habitat (Linsdale and Tevis 1951). Overhead branches and downed logs often provide woodrats with a means of traveling above ground level; this appears to be an important structural component of the habitat for some populations (as at Hastings Reservation) but not for others.

Woodrats radio-tagged by Sakai and Noon (1992b) sometimes moved in the evenings as far as 165 feet into old-growth forests adjoining their home ranges in shrublands. Sakai and Noon did not determine how long these woodrats remained in the old-growth, or what they did there, but generally they were back in their nests in the shrublands by the following morning. Two radio-tagged woodrats dispersed through old-growth forest from their natal home range into another shrubfield, in one case a distance of at least 650 feet. Such movements by woodrats would make them more available as prey for species like spotted owls that frequent these older forests.

Patterns of Abundance

Reported densities of dusky-footed woodrats range "from just a few animals to >40 per acre in early pole-timber stages, to perhaps 0.4 to 1.2 per acre in large saw timber and old growth" (Thomas et al. 1990, p. 207). In a corridor of habitat measuring approximately 100 by 1400 feet along an intermittent stream, Linsdale and Tevis (1951) trapped about 30 different individuals per month in one year and about 66 per month in another. These results suggest woodrat "densities" of about 9.3 and 20.6/acre-more than a two-fold difference between years. Densities in undisturbed habitats ranged from 2.1/acre in open woodlands of canyon live oaks and scattered Pacific madrones in the Santa Cruz Mountains, Santa Clara, County (Merritt 1974), to 18.3/acre in a riparian/hardwood forest of red alders, willows, and elderberries in coastal Sonoma County (Wallen 1982, Carraway and Verts 1991). Farther inland in Sonoma County, densities were 8.1/acre in late summer and 5.7/acre in winter in an undisturbed, riparian deciduous woodland dominated by red alder, California boxelder, and willows (Cranford 1977). In a study on the San Dimas Experimental Forest in the San Gabriel Mountains (Horton and Wright 1944), mean densities of woodrat houses were 4.6/acre in an area primarily of chaparral and oak woodland, 1-4/acre in chamise chaparral, 10/acre in riparian/hardwood communities, and 10/acre in unburned oak/chaparral and mixed chaparral above 4500 feet; a golden oak woodland with nearly complete canopy cover and almost no shrub understory had almost no woodrats. Chew et al. (1959) found 16 dead woodrats per acre in a burned canyon bottom dominated by oaks and California sycamores in south-coastal California.

Various studies have reported effects of habitat change on densities of dusky-footed woodrats. Woodrats declined significantly during a prolonged drought in the Santa Monica Mountains, Los Angeles County (Spevak 1983), and Linsdale and Tevis (1951) reported depressed numbers during a drought at Hastings Reservation. On the other hand, Kelly (1989) reported a dramatic population increase during a serious drought at Hastings Reservation in 1988. He attributed this to a large acorn crop in the autumn of 1987, possibly augmented by mild weather conditions. Removal of poison oak from the understory depressed population density in the Berkeley Hills, Alameda County (Vestal 1938); flood, browsing, and trampling of the understory by ungulates reduced woodrat numbers at Hastings Reservation (Linsdale and Tevis 1956). Following complete removal of shrubs from study plots in chaparral cover in coastal dunes near Morro Bay, San Luis Obispo County, a woodrat population declined sharply in the first 2 years following treatment and disappeared entirely by the third year. Areas undisturbed by fire had higher densities of woodrats than burned areas (Lee 1963, Gambs and Holland 1988). Studies by Wirtz et al. (1988), in an area of montane chaparral that burned in southern California, established that preburn densities of woodrats had not yet been reached 4 years after the burn. Postburn densities were higher in areas of light and normal burn than in areas with hot burns where all plant material was destroyed.

A suspected outbreak of plague in 1966-67 decimated woodrat populations in foothills of the southern Sierra Nevada, the Tehachapi Mountains, and the Coast Range (Murray and Barnes 1969).

Cranford (1977) reported significantly larger home ranges for males than females (0.59 vs 0.48 acre) in a riparian woodland bordered by grasslands and surrounded by redwood forest. Kelly (1989) found the same situation in riparian/hardwoods in Monterey County. Sakai and Noon (1992b) found a similar difference, though not statistically significant, among woodrats in shrubfields dominated by brushy tanoaks with an overstory of Douglas-fir in northwestern California. Depending on the spacing of nest clusters (color photo 5-25), females often shared portions of the same home range; consequently home ranges of breeding males can overlap those of several females.

Diet

The herbivorous dusky-footed woodrat apparently obtains most or all of its water from its food. It eats parts of a wide variety of plant species, but the water-rich leaves of thick-leaved shrubs found throughout the woodrat's range are probably the most important source of food. The bulk of the diet consists of leaves and the terminal shoots of twigs, with seasonally important food sources consisting of flowers, fruits (nuts, seeds, fleshy fruits, and so on) and fungi. Bark, wood, and other organic materials are also eaten occasionally. Fruits, fungi, and leaves are often cached within nests.

Linsdale and Tevis (1951) found that acorns and fruits of California coffeeberry were most numerous in caches examined at Hastings Reservation. Leaves and other parts of coast and canyon live oaks, California blackberry, chamise, California coffeeberry, buckbrush, and Jim brush were the major plants eaten. Somewhat less common in the diet were valley, blue, and black oaks; California wild rose; toyon; poison oak; Pacific madrone; and mountain whitethom. Parts of 56 other plant species were consumed (amounting to about 10 percent of the total diet), while 470 plant species (87 percent of the flora at Hastings Reservation) were not found in the diet of this woodrat.

In Joshua Tree National Monument, about 75 percent of the material in food caches in nests .consisted of shrub live oak and about 25 percent was California juniper (Cameron 1971). These proportions were the same even where the dusky-footed woodrat occurred together with the desert woodrat. The main foods in southern California coastal sage communities were lemonade sumac (fruit, seeds, vegetative parts), California buckwheat (vegetative parts), white sage (seeds, flowers, vegetative parts), and California scrub oak (leaves, fruits) (Meserve 1974).

Weights

Specimens from the western Sierra Nevada ranged in weight from 7.2 to 8.6 ounces (Grinnell and Storer 1924). Winter and summer weights in samples from foothill areas in San Diego County averaged 7.7 ± 0.7 and 6.5 ± 0.4 ounces, respectively (Stallone 1979). Sakai and Noon (1992b) reported a mean weight of 7.8 ± 0.14 ounces for a pooled sample of both sexes and all ages (*n* = 366) in Humboldt County. Adult males there averaged 10.7 ± 0.14 ounces (*n* = 101), and adult females averaged 8.5 ± 0.09 ounces (*n* = 133). At Hastings Reservation (Linsdale and Tevis 1951), adult males averaged 8.8 ounces (range 7.1-10.6) and adult females averaged 8.4 ounces (6.4-12.5). These rodents exhibit marked individual and seasonal variation in weight (table 10B). Immature woodrats weighing <5.3 ounces were trapped

Table 10B-*Weights (mean and range in ounces) of all ages of male dusky footed woodrats captured each month during a year at Hastings Natural History Reservation, Monterey County, California (adapted from Linsdale and Tevis 1951).*

Month	*n*	Mean	Range
January	68	8.9	7.0 - 12.0
February	67	9.3	4.9 -13.6
March	94	9.2	5.4 - 13.0
April	106	9.0	2.6 - 13.3
May	77	8.5	3.2 - 13.2
June	83	7.8	2.7 - 11.6
July	97	7.0	1.9 - 11.3
August	54	7.1	1.9 - 11.4
September	92	7.9	3.2 - 13.3
October	58	8.0	3.5 - 11.3
November	66	8.6	3.5 - 12.7
December	91	9.0	3.7 - 12.9

only between April and September. Immatures weighing from 3.5 to 7.0 ounces were trapped in all months but were taken most often in June and July.

Nests

Nests of sticks and other woody debris are typically located on the ground, occasionally in trees (color photo 5-23) or dense shrubs where support for the structure is available, and sometimes in rock crevices and abandoned human structures. Linsdale and Tevis (1951) summarized nest locations at Hastings Reservation as follows:

Most often	Bases of coast live oaks, California coffeeberry, willows, poison oak, California buckeye, California-laurel (bay).
Less often	Against logs, in rock outcrops (probably because of a lack of appropriate rocks or insufficient cover plants in areas studied-rocks are important in the San Gabriel Mountains and the southern Sierra Nevada), hollow cavities in trees (perhaps because of rarity and difficulty of detecting such nests), and among limbs of trees (trees with the right configuration of large and small branches to support nests may be preferred over the ground).

The structure of the plant community where nests were located at Hastings Reservation was described by Linsdale and Tevis (1951) as a mixed woodland with a mosaic of dense shrubs and trees, forming a complete and complex (multilayered) canopy:

Most often	Closed woodlands consisting predominately of coast live oaks (59 percent; n = 100).
Less often	Dense shrubs (28 percent), especially where California coffeeberry and poison oak were most abundant.
Rare (<10 pct)	Lone coast live oak trees (5 percent); live oak savanna (8 percent) (blue oak and valley oak savannas were not used for nests).

Nests are an important part of woodrat population dynamics. Nest clusters, occupied by related individuals, are common in favored habitats. Females, unlike males, stay in or near their natal area throughout their life, where related females breed in the same vicinity, living close together in kin clusters but in separate houses (Kelly 1989). In addition, individuals tend to cluster in favored habitat patches; consequently, such favored areas tend to become "crowded" over time (Linsdale and Tevis 1951). Vogl (1967) reported one adult per nest, but Sakai and Noon (1992a) have occasionally captured two adults per nest in northwestern California.

Reproduction and Development

Linsdale and Tevis (1951) found that 70 percent of the woodrats in their study area at Hastings Reservation survived less than 1 year, 27 percent survived 2 years, and 3 percent survived at least 3 years. Reproduction occurred in all months at Hastings, with the fewest pregnancies in December and the most in February. The number of juveniles appearing outside the nest was greatest in July and least (0) in January and February. Females were polyestrous, producing one to five litters per year, with one to four young per litter (mean about 2.5).

Forest Management

Fires, shrub removal, logging, and other human and natural disturbances generally reduce the suitability of woodrat habitat. Selective cutting of trees that opens the canopy and promotes growth of shrubby understory probably enhances habitat after several years, as do other logging techniques that promote successional stages with a complex mix of over- and understory trees and shrubs (Hooven 1959). The short-term effect, however, probably would be to reduce habitat suitability for woodrats. Although studies by Sakai and Noon (1992b) indicate that woodrats sometimes move from shrubfields into the edges of old-growth forests, it cannot be argued that logging to create openings would result in a net benefit for spotted owls in the conifer zone of the Sierra Nevada. First, available data from radio-tracking studies indicate that spotted owls seldom forage in shrubfields (Neal et al. 1989, Sisco 1990, Solis and Gutiérrez 1990, Zabel et al. 1992); and second, dusky-footed woodrats are generally uncommon as high as the mixed-conifer zone in the Sierra Nevada, where most logging currently occurs. Flying squirrels are the dietary staple of spotted owls in forests at these higher elevations, so logging there is more likely to have a negative effect on owl prey (via flying squirrels) than a positive one (via woodrats).

In forests below the Sierran mixed-conifer zone, small-scale logging operations might benefit spotted owls by enhancing woodrat populations. Although this needs further study, smaller sales might benefit spotted owls if done in areas adjacent to forested stands where the owls are known to forage. In such cases, woodrats that occasionally wander from their shrubby home ranges into the adjoining forest could become available as prey for spotted owls.

Woodrats do not survive fire well, especially very hot burns (Wirtz et al. 1988), and they are slow to recolonize burned areas (Longhurst 1978, Wirtz et al. 1988). Consequently, aggressive fuels management programs in chaparral country can benefit woodrat populations, especially in southern California where home ranges of owls in riparian/hardwood forests are closely surrounded by thick stands of chaparral (Chapter 5).

Northern Flying Squirrel

Distribution and Habitat

The northern flying squirrel is a medium-sized, nocturnal rodent that nests in trees in a great variety of forest communities over a broad, continental distribution. In California they occur in the North Coast, Klamath, southern Cascade, Sierra Nevada, and

Transverse Ranges. They are distributed throughout forested regions of the Sierra Nevada but apparently are more common in the mixed-conifer and red fir forests of the Pacific Slope than in the drier forests of the east slope. They are generally found above about 4,000 feet elevation in the Yosemite region and down to about 3,000 feet or lower in the northern Sierra Nevada, and in protected canyons and on north-facing slopes farther south. A single record from Chico is probably exceptional, but it suggests that flying squirrels may sometimes occur near the floor of the Central Valley in riparian/hardwood forests. Isolated populations also occur in the San Bernardino and San Jacinto mountains and probably in the San Gabriel Mountains of southern California.

Unfortunately, little published information is available on habitat associations or population levels of flying squirrels within the range of the California spotted owl. In the Sierra Nevada, common tree species associated with flying squirrels are black oak, white fir, and red fir. In the Lassen area, McKeever (1960) found flying squirrels in stands of ponderosa pine, lodgepole pine, and mixed stands of red and white fir. According to Waters and Zabel (1992), populations of flying squirrels have been located in second-growth stands of white fir at high elevation (about 6,300 feet) in the Lassen NF (color photo 5-1). These squirrels often travel and forage on the ground, so elements of the forest understory also are probably important in determining the suitability of their habitat.

In the San Bernardino Mountains, flying squirrels occur in mixed-conifer forests between about 5,200 and 7,500 feet in elevation (color photo 5-35). White fir and black oak are the principal tree species associated with these squirrels in the San Bemardinos (Grinnell 1908, 1933; Williams 1986). On a ridge south of Big Bear Lake, Summer (1927) caught 22 flying squirrels over the course of several months-all in white firs.

Stand size was an important attribute of suitable flying squirrel habitat in mature mixed-evergreen forests dominated by Douglas-fir on the Six Rivers NF. Northern flying squirrels were found in 60-80 percent of stands larger than 50 acres, on about 15 percent of stands of 25-50 acres, and on <10 percent of stands smaller than 15 acres (Rosenberg and Raphael 1986).

Sites with northern flying squirrels in isolated populations in the southern Appalachians varied markedly in plant community structure and composition (Payne et al. 1989). Occupied sites were commonly on north-facing slopes or in montane islands of conifer forests with cooler, mesic environments. Density of overstory trees varied from 364 to 1336 per acre; density of snags ranged from 11 to 138 per acre; and understory cover ranged from 35 to 86 percent. In a study of the southern flying squirrel in central Virginia, Sonenshine and Levy (1981) concluded that areas with few shrubs or vines as ground cover were unsuitable as habitat. An oak or oak-associated canopy with an understory of dense shrubs was optimal habitat. Presence of the squirrels was strongly correlated with shrub density. Although major differences exist in the distribution and habitats of northern and southern flying squirrels, the study by Sonenshine and Levy suggests that understory may be as important as tree canopy in determining habitat suitability.

Although Doyle (1990) captured similar numbers of flying squirrels in riparian and upland habitats, she concluded that riparian habitats were, nonetheless, superior to upland sites for flying squirrels. Waters and Zabel (1992) have found relatively high densities of flying squirrels in forest stands on the Lassen NF that are not near running water.

Patterns of Abundance

No published data are available on population densities, age structure, or reproduction in the Sierra Nevada or the mountains of southern California. A summary of most available literature indicated that "typical squirrel densities reported for mature and old-growth forests are 0.4 to 1.2 animals per acre" (Thomas et al. 1990, p. 205). Carey et al. (1992) found that flying squirrel density in southwestern Oregon was significantly greater in old-growth Douglas-fir stands (mean density = 0.8/acre) than in managed second-growth stands (mean = 0.4/acre). On the other hand, Rosenberg and Anthony (in press) failed to show significant differences between flying squirrel densities in old-growth (mean = 0.9/acre) and second-growth Douglas-fir stands (mean = 0.8/acre). Waters and Zabel (1992) found that average flying squirrel density was about 43 percent higher in late-seral red fir/white fir stands on the Lassen NF (range = 0.7-1.5/acre) than in red fir/white fir stands that were about 100 years old (range = 0.6-1.0/per acre). They have also found that flying squirrel density is strongly associated with the abundance of truffles-fruiting bodies of underground (hypogeous) fungi.

Diet

The diet of northern flying squirrels, at least as determined in California studies, consists primarily of truffles and arboreal lichens (McKeever 1960, Hall 1991, Waters and Zabel 1992), although they are known to eat a variety of other foods including seeds, nuts, insects, bird eggs and nestlings, and tree sap (Wells-Gosling and Heaney 1984). Maser et al. (1985) found that 90 percent or more of foods eaten in Oregon were fungi and lichens-hypogeous fungi accounted for more than 80 percent of the summer diet, and lichens comprised more than 50 percent of the diet year-round in northeastern Oregon. At Sagehen Creek, in the eastern Sierra Nevada, Hall (1991) found that spores of hypogeous fungi were the most common items found in feces and stomach samples year-round, but suspected that samples taken during deep snow cover indicated that the squirrels may store hypogeous fungi for consumption during winter months. Lichens and gill fungi were most prevalent during periods when snow covered the ground at Sagehen Creek. Hall considered arboreal lichens to be a very important winter food source for flying squirrels in areas with much snowfall (also see McKeever 1960). From studies of captive-reared animals, Laurance and Reynolds (1984) determined that winter diets consisting almost wholly of lichens may be more a matter of necessity than of preference for northern flying squirels. The captives selected pine seeds over lichens, moss, algae, and cones and branch tips from ponderosa pine.

Weights

Size varies significantly in a north-south cline along the Pacific Coast (Wells-Gosling and Heaney 1984), with the largest individuals in Alaska and British Columbia and the smallest in California. Weights of flying squirrels captured in Yosemite NP ranged from 3.62 to 5.76 ounces (Grinnell and Storer 1924). Juveniles captured in August and September in the Lassen NF averaged 2.89 ounces, and adults averaged 4.34 ounces (Waters and Zabel 1992). In a study by Witt (1991) in Douglas County, Oregon, the mean weight of adults captured between September 1983 and June 1984 was 4.7 ± 0.1 ounces (range = 3.7-6.5 ounces, *n* = 164). Generally the mean weight of adults was highest in January (mean = 5.0 ounces), dropping steadily to April, remaining stable from April through August (mean = 4.4 ounces), and increasing again through December.

Nests

Northern flying squirrels use several den sites; Carey (1991) found individuals in Oregon that used as many as seven. Two types of nests or dens are common-those located among branches of trees (for example, stick nests built by birds or other tree squirrels, clumps of dwarf mistletoe, and moss), and those located in natural cavities in trees and snags or abandoned woodpecker holes (Wells-Gosling and Heaney 1984). In Oregon, live conifers with cavity nests averaged 49 inches in d.b.h.; snags with cavity nests averaged 35 inches in d.b.h. (Carey 1991). Nests in such cavities are probably important in areas with cold winters (Cowan 1936, Weigl 1978), although Waters and Zabel (1992) have found populations of flying squirrels in high-elevation (about 6,300 feet) stands of second-growth white fir where few snags or cavities occurred. We do not know how commonly flying squirrels build their own nests.

Reproduction and Development

Litters commonly consist of two to four young, rarely one to six (Wells-Gosling and Heaney 1984). In Yosemite NP, females with two to four embryos were found in June (Grinnell and Storer 1924). Young are born between mid-June and mid-August in Oregon (Carey 1991). Weaning occurs at an age of about 60 days. Carey reported that young in an Oregon study were not weaned until mid-October to mid-November; they either dispersed in autumn or spent the winter in the nest with their mother. Young can walk and begin to leave the nest when about 40 days old. Most yearling females did not breed, and about 25 percent of the adult females did not breed in a given year. Although several authors have suggested that more than one litter is produced per year (Grinnell and Storer 1924, Witt 1991), a single litter is probably more common, at least throughout the Sierra Nevada (Waters and Zabel 1992). In the Sierra Nevada, two "half-grown" young were captured on 31 October, and a "quarter-grown" young was found on 16 September (Grinnell and Storer 1924, p. 214).

Forest Management

Habitat features that most strongly influence flying squirrel abundance include: sufficient trees to enable efficient locomotion; nest and den site substrates (cavity-bearing trees and snags), and truffle and arboreal lichen biomass. Although flying squirrels can glide at least 155 feet (Mowrey and Zasada 1984, J. R. Waters pers. observ.), forestry practices that create openings wider than about 120 feet probably have a negative effect on flying squirrel locomotion. Tree height is also important. Flying squirrels cannot glide as far from small trees as they can from tall ones.

As cavities provide important nest and den sites, efforts should be made to leave cavity-bearing trees and snags. In areas lacking potential nest sites, it may be possible to increase flying squirrel populations by adding nest boxes.

Truffles and arboreal lichens are the most important food types for flying squirrels throughout California and in the Pacific Northwest. Arboreal lichens are especially important as a winter food resource. Forest practices that reduce truffle and lichen biomass will probably negatively impact flying squirrel abundance. Ongoing research by Waters and Zabel (1992) indicates that truffle biomass is strongly associated with the presence of a well-developed soil organic layer and the volume of decaying logs (color photos 5-7, 5-18, and 5-34). Forest practices that negatively impact those parameters, such as broadcast burning and bulldozer piling after logging (Harvey et al. 1980), will reduce the capability of the forest to sustain flying squirrels. Data from Waters and Zabel (1992) also show that arboreal lichens (in the genera *Letharia* and *Bryoria)* commonly eaten by flying squirrels are much more abundant in older red fir/white fir forests than in younger forests.

Management of conifer forests in the Sierra Nevada for flying squirrels should emphasize retention of large snags and older trees, and nonintensive site-preparation techniques.

Pocket Gophers

Distribution and Habitat

Two species of pocket gophers occur within the main geographic range of the California spotted owl. Mountain pocket gophers range from the Mt. Shasta Region southward in the Sierra Nevada to at least the northern boundary of Tulare County (Hall 1981). They generally occur from above 6,900 feet in the Sierra NF (5,600 feet in the Stanislaus NF and Yosemite NP) to slightly above timberline (Grinnell and Storer 1924; D. F. Williams, pers. observ.). They are found throughout subalpine areas of both Sequoia and Kings Canyon NPs (Graber, pers. comm.), generally at elevations above 8,500 or 9,000 feet that are not frequented by spotted owls. They are most common in deeper, drier soils around meadow margins, but they occur everywhere except on bare rock and within closed-canopied, mature and older forests with little or no herbaceous ground cover (Ingles 1952).

Southwestern pocket gophers occur in the western Sierra Nevada at elevations below the mountain pocket gopher, and in the lowlands, mountains, and deserts of western and southern California and northern Baja California. They probably range to timberline in the southern Sierra Nevada, from Tulare County southward. Distribution records of pocket gophers above 6,900 feet in the southern Sierra Nevada are unavailable, although one or the other species surely is found there (Hall 1981). Southwestern pocket gophers are most common on open ground with well-drained soils supporting grasses and forbs, but they can be found everywhere except on bare rock and in closed-canopied, mature and older forests.

Great Basin pocket gophers occur on the eastern slopes of the Sierra Nevada and on the Modoc Plateau. We do not discuss them in detail here because they probably occur mostly outside the breeding range of the California spotted owl, and because features of their population dynamics, habitat, and diet that are of importance to spotted owls probably do not differ from those of other pocket gophers. Generally, the ranges of these three species of pocket gophers do not overlap.

Patterns of Abundance

Mean density of mountain pocket gophers in favored meadow habitats was estimated at 10/acre in autumn over a 4-year period (Ingles 1952). The lowest estimates were in summer and autumn 1950 (4/acre), the highest in summer 1949 (19/acre). Biomass of mountain pocket gophers fluctuated from a low of 27.7 ounces/acre in spring 1948 to a high of 46.3 ounces/acre in summer 1949; this had dropped to an estimated 11.8 ounces/acre by the following summer.

In favored habitat at the San Joaquin Experimental Range (SJER), Madera County, the density of breeding adult southwestern pocket gophers averaged about 2.0/acre over five breeding seasons. Numbers of young produced by these adults averaged 2.3/acre over four breeding seasons (estimates from figures in Howard and Childs 1959, p. 340). Near Bass Lake, Madera County, in a Sierran mixed-conifer forest (about 4,500 feet), the density on a plot that included cutover forest and meadows was 4.6/acre, but Storer et al. (1944) believed this to be only half or less of the actual population.

General Life History Features

Pocket gophers are solitary and territorial, normally not ranging beyond the boundaries of their territories. They are most active early in the morning and late in the day, near sundown; at the highest elevations, most activities occur in late afternoon and evening. They are fossorial creatures, digging and living in underground tunnels, and creating many shallow, foraging tunnels about 5 inches below ground level. Their burrow entrances are plugged with dirt except when the gophers are pushing dirt from excavations to the surface, foraging on plants around the burrow entrance, or searching for mates. During excavation and while foraging on plants at the surface, they usually expose no more than the anterior half of their body at the burrow entrance.

Most burrowing activities occur during the cooler, wetter months in western California. At lower elevations, little or no burrowing occurs during the dry summer period, when gophers retreat to their few, deeper tunnels and plug the shallow ones. They may subsist mainly or entirely on cached food during this period. At higher elevations, when snow covers the ground, pocket gophers come to the surface and burrow through the snow to reach food plants, often packing these tunnels with dirt from underground excavations.

Burrow systems of neighbors typically are discrete. Any interconnections that may be accidently established apparently are kept plugged with dirt. Hearing may play a role in preventing encroachment by neighbors (Ingles 1952).

Soil, plant cover, and seasonal flooding are the principal factors determining habitat suitability and density of these pocket gophers. Areas with waterlogged soil and sites of seasonal flooding are unsuitable as permanent habitat. At SJER, at an elevation of about 1,000-2,000 feet in the western foothills of the Sierra Nevada, the strongest correlation with abundance of pocket gophers was soil depth (Howard and Childs 1959). Gophers were not found living in soils shallower that about 12 inches, and were most abundant in soils at least 24 inches deep. Areas with the deepest soils showed the highest above-ground productivity of herbaceous plants.

Mean weights of female pocket gophers were greater in sites with deep soils compared to sites with shallow soils, but differences were not statistically significant. Pocket gophers living in irrigated fields are significantly larger and heavier than their genetically identical neighbors in natural communities (Howard and Childs 1959, Patton and Brylski 1987). Areas supporting an abundance of grasses and forbs, especially species forming underground rhizomes, corms, tubers, bulbs, and other storage organs, provide the greatest habitat values for food. Areas with dense or complete canopy cover of woody shrubs and trees provide the poorest habitats for pocket gophers.

Diet

Pocket gophers eat a variety of plants, favoring herbaceous over woody material. Food not immediately consumed is cached in underground larders. Much of the information on diet comes from examination of these caches. Most species of grasses and forbs known to occur in a foothill oak-pine savanna at SJER were found in caches of southwestern pocket gophers. Seeds, tubers, bulbs, rhizomes, and acorns also were found in the caches (Howard and Childs 1959). Mountain pocket gophers near Huntington Lake, on the Sierra NF, also ate a wide variety of plants. During snowless months, caches of corms and roots of meadow bitterroot and golden brodiaea were found in caches. In winter, mountain pocket gophers cached mountain whitethorn leaves in snow tunnels, and the parts of willow stems covered with snow were frequently gnawed (Ingles 1952).

Weights

Microgeographic, seasonal, and annual variations occur in weights of adult pocket gophers. Season, sexual activity, and habitat quality have major influences on size and mass of adults (Howard and Childs 1959, Daly and Patton 1986, Patton and Brylski 1987). Mean weights of mountain pocket gophers in a Sierra Nevada meadow ranged from 2.2 (lowest summer average) to 3.1 ounces (highest spring average). Nonbreeding animals in autumn averaged from 2.2 to 3.0 ounces in different years (Ingles 1952). Weights of southwestern pocket gophers at SJER varied as follows (Howard and Childs 1959, fig. 11).

Females 8-10 months of age--mean = 2.2 ounces (range 1.8-2.6).
Females 20-22 months of age--mean = 2.6 ounces (range 2.2-3.1).
Males 8-10 months of age--mean = 3.2 ounces (range 2.3-8.8).
Males 20-22 months of age--mean = 4.3 ounces (range 3.9-4.7).

Mean weights of trapped animals were highest in spring and lowest in summer and autumn.

At Hastings Reservation, modal weights of trapped males were between 4.0 and 4.4 ounces, with a range of about 2.1 (juveniles) to 7.7 ounces (largest adults). Modal weights of trapped females were between 3.2 and 3.9 ounces, with a range from about 1.9 (juveniles) to 4.7 ounces (largest adults) (Daly and Patton 1986, fig. 3).

Reproduction and Development

Mountain pocket gophers begin breeding in May or June and young are born in June to August. Only one litter of three or four young per year is the norm. From about mid-July to early September, young disperse over the ground surface until a suitable site is found (Ingles 1952). Often burrow systems established by dispersers are in marginal or unsuitable habitats, such as shallow, sterile, granitic soils, or in small plots of higher ground surrounded by waterlogged soil. Some adults and young of the previous year apparently disperse in winter through snow tunnels. Dispersing adults are predominately males.

Based on studies by Howard and Childs (1959), southwestern pocket gophers at SJER commenced breeding in January, considerably earlier than is the case with the mountain pocket gopher. Most females were first pregnant the last 2 weeks of February; mean litter size there was 4.6. The young dispersed from March to May, although both young and adults occasionally moved over the ground at other periods of the year. Females born in January sometimes produced litters in April or early May of the same year. Most females produced only one litter per year, but a few had two. Between 50 and 75 percent of the females in January 1950-1954 were young of the previous breeding season (9-11 months old).

In a mixed-conifer forest at an elevation of about 4,500 feet, near Bass Lake, Madera County, scanty data suggest that young are born in early July and that some females may have two litters, similar to populations of this same species at lower elevations (Storer et al. 1944).

In a montane woodland community at Hastings Reservation, southwestern pocket gophers began breeding after onset of the winter rainy season, usually by January (Daly and Patton 1986). The breeding population was composed of animals at least 7-8 months old. Most females probably had only a single litter.

The breeding season of southwestern pocket gophers in the San Bernardino Mountains, at an elevation of about 7,500 feet near Bear Lake, is probably similar to that of mountain pocket gophers in the Sierra Nevada (Grinnell 1908).

Estimated survival of southwestern pocket gophers to 1 year of age ranged from about 5 to 40 percent for males and 15 to 50 percent for females between 1949 and 1953 (Howard and Childs 1959). Less is known about mountain pocket gophers, but 34 percent of the individuals in autumn populations in the Sierra NF were young of the year, and little turnover was detected in the spring breeding populations of 1949 and 1950 (Ingles 1952).

Forest Management

Generally, actions that tend to benefit pocket gophers would tend to lessen overall habitat suitability for spotted owls, so we would not recommend any active management to increase the amount of suitable habitat for gophers. Natural and man-made openings in the forest will undoubtedly occur with sufficient regularity to assure that these burrowing mammals will continue to be available as prey for California spotted owls.

White-Footed Mice

Distribution and Habitat

Five species of white-footed mice (genus *Peromyscus*) occur within the range of the California spotted owl. Indeed, white-footed mice are nearly ubiquitous in terrestrial habitats and often one or another species in this group is the most abundant small mammal. They exhibit considerable geographic variation in habitat associations, so results of studies on a given species in one locality should not be too broadly applied. Because of its marginal occurrence with the California spotted owl, we do not include the cactus mouse in this review.

Brush Mouse

Brush mice range throughout most of the area inhabited by California spotted owls, although they are absent from most of the inner coastal ranges (Diablo Range) of central California south of Suisun Bay and north of the Transverse Ranges in Kern and Santa Barbara Counties. They are relatively scarce above 3,500 feet in the northern portion of the western Sierra Nevada (Grinnell et al. 1930), but may occur higher in chaparral and other shrub associations on south-facing slopes (Jameson 1951). They occur up to about 5,100 feet at the level of the Sierra NF. On the Pacific slopes of the San Gabriel Mountains, brush mice occur mainly between 1,600 and 6,000 feet, where they show decided preferences for rocky sites in oak woodlands, riparian/ hardwood communities, and mixed-species chaparral (Vaughan 1954). Brush mice climb readily and are often seen or captured in trees. They are not known to hibernate or to enter torpor.

Brush mice may construct nests in hollows in trees or in ground burrows. They are closely associated with oaks and rocky sites. At Pinnacles National Monument in the Gabilan Range, Monterey County, brush mice comprised only 5 percent of the white-footed mice captured in a complex mix of woodland, chaparral, and grassland communities. They were significantly associated with poison oak and medium-sized rocks (10-50 inches), and they showed a significant negative association with grass (Fellers and Arnold 1988). Elsewhere they are typically the most common white-footed mouse where rocks and oaks occur together in oak woodlands and forest communities below the mixed-conifer zone. In the central Sierra Nevada (Yosemite NP), oaks and proximity to water were commonly associated with brush mice (Grinnell and Storer 1924). Other researchers have not verified a dependence on surface water; possibly exposed rocks in canyon bottoms and shrubby growth along streams provide suitable habitat in otherwise inhospitable surroundings. At SJER, an area with no permanent streams, brush mice were the most common species of white-footed mouse, preferring rocky areas sheltered by oaks (Quast 1954). They were also the most common species in the La Panza Range of San Luis Obispo County, with nearly equal abundance in blue oak woodland, mixed chaparral (chamise, ceanothus, and scrub live oak), and the ecotone between these communities along canyon bottoms (Murray 1957).

California Mouse

California mice occupy chaparral and woodland communities in western California and northern Baja California, south of San Francisco Bay on the Coast, and from Mariposa County southward in the Sierra Nevada foothills. Their elevational distribution in the Sierra Nevada is generally from the lower half of the ponderosa pine forest downslope to the mid-elevation, oak-pine woodlands and chaparral. Elevational limits in the mountains of southern California are generally below about 4,900 feet, with an exceptional record at 7,900 feet in the San Jacinto Mountains (Grinnell 1933). California mice climb readily and are frequently captured in traps set in shrubs and trees (Meserve 1976a, 1977). They may become torpid on a diurnal cycle when deprived of food (Hudson 1967).

California mice have more specialized habitat requirements than brush and pinyon mice, preferring broadleaved woodlands and mixed chaparral and being more limited in their elevational and latitudinal distributions. Within their geographic range, they are closely associated with the distribution of both dusky-footed woodrats and California-laurel (bay), although both associates occur much farther north than California mice (Merritt 1974). Plant communities inhabited include valley foothill hardwood and oak-pine woodlands, various chaparral associations, and riparian deciduous. Within preferred habitat, California mice are often the most abundant small mammal species. At Pinnacles National Monument, California mice accounted for 10 percent of all captures of white-footed mice. They were absent from areas of extensive grass and large patches of chamise chaparral. Variables most strongly associated with the presence of this species were hollyleaf cherry, medium-sized rocks, and Chinese nests (a wildflower) (Fellers and Arnold 1988). They are among the commonest rodent species in mixed-chaparral communities in the San Gabriel Mountains below about 4,900 feet (Vaughan 1954, Wirtz et al. 1988). In coastal sage communities, they are generally limited to thickets of large shrubs and small trees in riparian/hardwood stands (Vaughan 1954). M'Closkey (1972) captured only six residents in coastal sage scrub and their mean duration on plots was less than half that of cactus and deer mice. He believed their occurrence on the study plot was due to previous flooding of their preferred habitat along washes where trees and large shrubs were found.

California mice often nest in abandoned or occupied stick nests of dusky-footed woodrats. They also may nest in hollows in trees, snags, or logs, and they construct stick nests of their own, often under fallen logs and smaller downed woody material (Merritt 1978). They apparently do not burrow readily; many researchers have proposed that their distribution and abundance are limited by availability of suitable nesting sites (Merritt 1974, 1978).

Deer Mouse

Deer mice occur throughout the range of the California spotted owl, and in most plant communities, from marshes and grasslands at or below sea level, through woodlands and forests, to above timberline in the mountains. Within this broad area, however, they are generally common only in riparian/hardwood and grassland communities at lower elevations, and riparian, forest, and meadow communities from the mid-elevation mixed-conifer zone upslope through lodgepole and subalpine pine forests. Deer mice probably are the most terrestrial of the white-footed mice considered here (King 1968; Meserve 1976a, 1977). Meserve (1977) seldom found them in shrubs or trees in a southern California community of coastal sage, even though they can climb readily and are taken in traps set in brush and trees. Torpor under natural conditions is unknown for deer mice.

Deer mice typically nest in ground burrows, hollow logs, or talus. Nests are less frequently located in hollows of trees and snags. They are generally much less common than brush and pinyon mice in ponderosa pine, oak-pine woodlands, foothill and montane hardwood forests, and chaparral on the western slopes of the Sierra Nevada (for example, tables l0A and l0C; Quast 1954), in the coast ranges, and in mountains of southern California. Within these communities, they are most often found in riparian deciduous associations, wet and dry meadows, and grass/forb seral stages. In the northern Sierra Nevada, deer mice were significantly more abundant in forested than in shrub stages of mixed-conifer forest (Jameson 1951). In coastal woodland and chaparral communities, deer mice are uncommon and usually associated closely with riparian/hardwood communities or large openings dominated by annual grasses and forbs. At Pinnacles National Monument, deer mice comprised 20 percent of the white-footed mice captured in a complex of grassland, oak, pine, and chaparral communities. Most captures were on burned

Table 10C-*Captures of small rodents that may be prey of California spotted owls, by successional stage (after Verner and Boss 1980)1 in forest communities of the western Sierra Nevada, Sierra NF (D. F. Williams pers. observ.). Total adjusted sampling effort was 18,200 trap days (one trap day = one pitfall trap set for 24 hours). Trapping was simultaneous in all forests and successional stages. Values are actual captures, except "catch rate," which is the number captured per trap day. Captures were standardized to represent equal sampling effort in the various habitat types. (Most habitat types/stages were sampled on two transects of 10 traps each, set for 7 days in 1980 and 28 days in 1982. LTB in ponderosa pine, GF in mixed-conifer, and LTC in red fir forests were sampled only on single transects, so numbers of actual captures there were doubled.)*

Forest community and mammal species	Habitat type/stage									Total	Catch rate
	GF	SSS	PMA	PMB	PMC	LTA	LTB	LTC	RH		
Ponderosa pine											
Southwestern pocket gopher	1	1	2	0	0	2	0	--	1	7	0.0013
Deer mouse	12	0	0	0	1	1	2	--	1	11	0.0020
Brush mouse	3	2	3	0	0	1	8	--	10	27	0.0048
Pinyon mouse	0	6	4	6	13	13	0	--	0	42	0.0075
California vole	2	0	0	0	1	0	0	--	1	4	0.0007
Total	**18**	**9**	**9**	**6**	**15**	**17**	**10**	**--**	**13**	**91**	**0.0188**
Mixed-conifer											
Southwestern pocket gopher	0	0	1	1	0	0	0	0	0	2	0.0003
Deer mouse	2	21	14	3	6	7	12	11	29	105	0.0167
Brush mouse	0	0	0	0	1	0	0	1	2	4	0.0006
Pinyon mouse	0	0	1	2	0	0	0	0	0	3	0.0005
Long-tailed vole	0	12	4	1	0	0	1	0	7	25	0.0040
Total	**2**	**33**	**20**	**7**	**7**	**7**	**13**	**12**	**38**	**138**	**0.0221**
Red Fir											
Mountain pocket gopher	6	1	1	0	0	0	0	2	4	15	0.0024
Deer mouse	40	30	9	15	12	14	15	10	42	187	0.0300
Long-tailed vole	5	6	0	5	1	1	5	0	40	63	0.0100
Total	**51**	**37**	**10**	**20**	**13**	**15**	**20**	**12**	**86**	**265**	**0.0424**

[1] GF = grass/forb; SSS = shrub/seedling/sapling; PMA = pole-medium tree with <40 percent canopy cover; PMB = pole-medium tree with 40-69 percent canopy cover; PMC = pole-medium tree with >69 percent canopy cover; LTA = large tree with <40 percent canopy cover; LTB = large tree with 40-69 percent canopy cover; LTC = large tree with >69 percent canopy cover; RH = riparian/hardwood community in corresponding forest zone.

areas and in a grassy field. Variables positively associated with their occurrence were chamise and bird's foot trefoil (together), and yerba-santa. Percent cover of oak leaf litter was negatively associated with deer mice (Fellers and Arnold 1988).

In the San Bernardino Mountains, brush mice outnumbered deer mice on mixed-conifer plots at elevations between 5,800 and 7,000 feet, but deer mice were more abundant on mixed-conifer plots at 7,600 feet (Kolb and White 1974). Grinnell (1908) found deer mice common only in big sagebrush on the desert slopes and high ridges, and in montane forests above 6,900 feet. Deer mice were not captured by Spevak (1983) at four sites in the Santa Monica Mountains, Los Angeles County, in chaparral, riparian, and coastal sage associations. Yet Price and Kramer (1984) caught small numbers in a variety of microhabitats in a coastal sage community in Riverside County. M'Closkey (1972) also captured deer mice in a coastal sage community in Orange County and noted that they were the most general in habitat preference, being found along the moisture gradient from grasslands to woodlands. In mixed montane-chaparral communities of the Pacific slopes of the San Gabriel Mountains, deer mice were absent from chaparral that had not been burned for several years but were present on all burned plots, with peak numbers occurring 2 years after burns (Wirtz et al. 1988).

Pinyon Mouse

Pinyon mice also occur throughout the area inhabited by California spotted owls, but generally range below the mixed-conifer forests on the western slopes of the Sierra Nevada. They are associated with oak-pine woodlands and chaparral communities, usually with one or more species of conifers such as juniper, pinyon pine, or digger pine. They are less common in ponderosa pine habitats, where they most often occur on hotter, drier slopes in association with chaparral or in more mature stages of forest. In southern California they are generally uncommon or only locally distributed on the Pacific slopes of the mountains. Vaughan (1954) found none on the Pacific side of the San Gabriel Mountains. In the San Bernardino Mountains, Grinnell (1908) captured them only at two localities on the Pacific side. One was a south-facing slope at 6,500 feet vegetated with Coulter pine, chamise, deer brush, curlleaf mountain mahogany, and California scrub oak-plants typical of the upper-elevation chaparral of the Pacific side, and pinyon pine and western serviceberry-plants more typical of the desert side. The other was a south-facing slope where pinyon mice were taken between 5,100 and 5,500 feet among a mix of plants of upper-elevation chaparral and lower-elevation forest (ponderosa pine, white fir, and black and canyon live oaks). Chaparral plants predominated. Pinyon mice readily climb and are frequently taken in traps set in shrubs and pygmy conifers (for example, juniper, pinyon pine, digger pine, Coulter pine).

Pinyon mice nest in ground burrows or hollows in trees. They apparently do not become torpid. In the central coastal chaparral, woodland, and forest communities, they are common wherever shrub or tree cover is found, especially with one or more species of pygmy conifers or dense stands of chamise or ceanothus chaparral (or a mix of these and other shrubs). Pinyon mice were the most abundant small mammal trapped in chamise chaparral at Hastings Reservation (Bradford 1976). At Pinnacles National Monument, pinyon mice accounted for about 66 percent of the white-footed mice captured in a variety of oak, pine, grass, and chaparral associations. They were found in all community types but grassland. Large rocks and various shrub species were significantly associated with occurrence of pinyon mice. Grasses and forbs indicated the poorest habitats (Fellers and Arnold 1988). In the Sierra Nevada, they are mostly limited to areas with dense brush or tree cover below about 4,600 feet, and are usually abundant only where oaks do not dominate. At SJER, pinyon mice were commonly associated with moderate to dense stands of brush, particularly buckbrush, and rocks. Likewise, in the southern Sierra Nevada (Kern County), pinyon mice preferred stands of buckbrush and rock outcrops (Lawrence 1966). In the La Panza Range of San Luis Obispo County, they were more than four times as common in a chaparral community of chamise, buckbrush, and coast live oaks as they were in a blue oak/digger pine woodland (Murray 1957). None was taken in chaparral communities in over a decade of studies on the San Dimas Experimental Forest, on the Pacific slope of the San Gabriel Mountains (Wirtz et al. 1988).

Patterns of Abundance

Results of trapping suggest some differences in habitat affinities of white-footed mice in the western Sierra Nevada (tables l0A and lOC). Deer mice were captured in most habitat types and seral stages, exhibiting apparent specialization at low elevations (where brush and pinyon mice co-occur) in sites dominated by grasses and forbs. Their habitat associations increase markedly with increasing elevation to the point that they are ubiquitous in the red fir zone, where no other species of white-footed mice occur. Pinyon mice were generally confined to sites with shrubs, mixtures of shrubs and small trees, or shrubs and widely scattered trees in all habitats sampled except the oak/digger pine type, yet other studies (Quast 1954, Block et al. 1988) found them to be common in this woodland type, where they were associated with shrubs. Brush mice were relatively uncommon in most habitats, except those at lower elevations that had large trees in the canopy. California mice were essentially missing from the sample, although study sites were either too far north for this species or generally in habitat types where we would not expect to find them.

Any interpretation of habitat use reported in tables 10A and 10C should note differences in elevation and forest composition. Sierran mixed-conifer sites reported in table 10A, for example, were mostly on north-facing slopes of canyons 2,000-3,900 feet in elevation, where Douglas-fir occurred with ponderosa pine, sugar pine, incense-cedar, or black oak. Studies reported in table IOC were farther south, at elevations of 5,200-6,500 feet. Douglas-fir was rare there, and most sites had white fir mixed with the other species listed above.

Densities of white-footed mice within the range of the California spotted owl generally fluctuate between lows in December and January to highs in July and August. At higher elevations in mixed-conifer and fir forests, annual peaks in densities may be delayed into August or September. Densities of different species vary from <1 to >30 mice/acre. Various density estimates have been reported in the literature; these are summarized below (animals/acre), but readers should be mindful of the problems with estimating densities of small mammals and the variety of methods used.

Brush mice-1.0-15.3 (Zeiner et al. 1990); 3.0-15.2 (Sierran mixed-conifer, Bass Lake area, Storer et al. 1944); 1.3 (Lake Tahoe area, Storer et al. 1944).

California mice-31.2 (xeric chaparral, central California, Merritt 1974); 37.2 (mesic oak-laurel forest, central California, Merritt 1974); 0.1-0.8 and <0.8 (southern California coastal-sage scrub, MacMillen 1964 and M'Closkey 1972, respectively).

Deer mice-4.0-10.0 (White et al. 1980); 4.9-14.2 (mixed-conifer forest,Sierra Nevada, Bass Lake area, Storer et al. 1944); 19.1 (Lake Tahoe area, Storer et al. 1944), <0.4-1.6 (southern California coastal sage, M'Closkey 1972).

Pinyon mice-1.0 (oak-laurel forest, central California, Merritt 1974); 34.8 (xeric chaparral, Merritt 1974).

General Life History Features

White-footed mice are nocturnal and active throughout the year. Some species become torpid under food or water deprivation, but others do not. They nest in ground burrows, talus, hollow logs, and in hollows in trees. They readily climb in brush and trees (scansorial). Arboreal tendencies differ among species, however, with brush and California mice being the most scansorial of the species occurring in California, and deer mice the least. White-footed mice are not highly territorial except near their nest, but territoriality differs among species. The California mouse is the most territorial species, living in male-female pairs with nearly nonoverlapping home ranges (Ribble and Salvioni 1990).

Diet

White-footed mice are omnivorous, feeding on seeds, fruits, fungi, flowers, foliage, insects and other arthropods, carrion, and other animal matter (Zeiner et al. 1990). Specific studies suggest that the four species considered here are largely opportunistic in choice of diet, although differences are seen where species' ranges overlap (for example, Jameson 1952; Meserve 1976a, 1976b). Insects (especially larvae and pupae), seeds, fruits, and fungi probably comprise the bulk of their diets. California mice eat large quantities of California-laurel seeds, the thick, hard coats of which cannot be cracked by pinyon mice (Merritt 1974). In a coastal sage community, California mice ate mostly shrub fruits, seeds, and flowers and smaller quantities of grass seeds (Meserve 1976a).

Reproduction and Development

Reproduction varies geographically, altitudinally, and annually. Females appear to be seasonally polyestrous, with most births occurring between March and October, but some females may be pregnant in any month. The most prolonged reproductive seasons are found in populations at or near sea level and on the lower slopes of coastal ranges. The shortest reproductive seasons occur at the highest elevations in montane communities.

The breeding season of brush mice peaks in April and May; a secondary peak in June to August seems to depend upon the previous crop of acorns. Litters average three to four young; females probably average near two litters per year, although they can have four. Females born in spring can breed in the summer of their first year.

Although California mice may breed year-round in coastal areas, most breed between March and September. Litter size averages two to three (MacMillen 1964, Merritt 1978), with up to three to four litters per year. Females born early in the year breed late in the reproductive season of the same year, although California mice mature more slowly than the other white-footed mice considered here.

Deer mice may breed year-round, depending upon climate, but most reproduce between March and October. Litters are l arger at higher elevations and latitudes, but probably average four to six for populations within the range of the California spotted owl. Numbers of embryos for 46 females from the Sierra NF, most captured between mid-June and mid-August in mixed-conifer and red fir forests, averaged 5.2 ± 1.43 (range = 2-9). Mean litter size for 11 females in a southern California coastal-sage community was 4.3 ± 1.3 (MacMillen 1964). Females may have two to four litters during the breeding season-fewer at higher elevations and latitudes. Young born in spring breed later in the same summer or autumn.

Pinyon mice breed mainly from May to September, averaging two to three young per litter. Females may breed when 3 months old.

Little information is available on dispersal by these species within the geographic range of the California spotted owl. Dispersal probably commences soon after weaning, but individuals may leave their natal homes over a protracted period, depending upon circumstances such as survival of the mother, population density, and food abundance. Time to weaning varies geographically and by species. For brush and deer mice, weaning probably averages about 25 days (range of reported values, 22-37 days, summarized by Zeiner et al. 1990). California mice are weaned in an average of 35 days, although some litters may not be weaned until 44 days (McCabe and Blanchard 1950, Merritt 1974). Clark (1938) reported 50 days as the period before weaning in pinyon mice, although other studies found considerably shorter periods-about 25 (McCabe and Blanchard 1950) or 30 days (Douglas 1969).

Weights

The deer mouse is the smallest of the four species considered here. Adults (excluding pregnant females) weigh about 0.53-0.91 ounces (Layne 1968); the mean for a Sierra Nevada sample was 0.70 ± 0.01 ounces, *n* = 144. Grinnell and Storer (1924) listed a range of 0.45-0.74 ounces for deer mice caught in the central Sierra Nevada.

Adult brush mice ranged in weight from about 0.77 to 1.19 ounces in the Yosemite region (Grinnell and Storer 1924). The mean of a mixed-age sample of brush mice in the Sierra NF varied from about 0.74 to 0.95 ounces (table 1013).

Breeding adult pinyon mice from central coastal California averaged 1.19 ± 0.11 ounces (Merritt 1974). The range of weights in the Yosemite region was 0.82-1.44 ounces (Grinnell and Storer 1924). Samples of breeding adults from the Sierra NF averaged about 0.98-1.09 ounces.

California mice are the largest of the white-footed mice in California. Most reported adult weights range from about 1.33-1.75 ounces (Grinnell and Storer 1924, Layne 1968, Jameson and Peters 1988). Merritt (1974) reported mean weights of breeding adults as 2.0 ± 0.28 ounces in central coastal California. A population mean for all ages and sexes captured year-round in a coastal-sage community in southern California was 1.20 ounces (MacMillen 1964).

Table l0D-*Variation in weights (in ounces, mean ± SD, with range and sample size below) of three species of white footed mice during summer (June-August, Sierra National Forest, Fresno County) and winter (January, San Joaquin Experimental Range) (D. F. Williams pers. observ.).*

Season	Sample	Brush mouse	Deer mouse	Pinyon mouse
Summer	Adults	0.99 ± 0.11	0.74 ± 0.13	1.00 ± 0.07
		(0.74 - 1.33)	(0.46 - 1.12)	(0.77 - 1.30)
		n = 39	*n* = 208	*n* = 31
	Young	0.51 ± 0.08	0.43 ± 0.09	0.54 ± 0.12
		(0.41 - 0.63)	(0.21 - 0.56)	(0.39 - 0.77)
		n = 5	*n* = 113	*n* = 12
	Pooled	0.93 ± 0.18	0.63 ± 0.19	0.87 ± 0.24
		(0.42 - 1.33)	(0.21 - 1.12)	(0.39 - 1.30)
		n = 44	*n* = 321	*n* = 43
Winter	Adults	0.78 ± 0.07	0.54 ± 0.07	0.90 ± 0.13
		(0.67 - 0.95)	(0.39 - 0.70)	(0.70 - 1.09)
		n = 31	*n* = 14	*n* = 9
	Young	0.61 ± 0.03	0.49 ± 0.07	0.57 ± 0.08
		(0.56 - 0.67)	(0.35 - 0.60)	(0.49 - 0.67)
		n = 12	*n* = 13	*n* = 5
	Pooled	0.73 ± 0.10	0.51 ± 0.08	0.78 ± 0.20
		(0.56 - 0.95)	(0.35 - 0.70)	(0.45 - 1.09)
		n = 43	*n* = 27	*n* = 14

Management

Clearcutting or similar tree harvest and brush thinning or removal generally result in increased numbers of deer mice. Wildfires and controlled burns that reduce shrubs and small trees and increase cover of grasses and forbs also enhance populations of deer mice in woodland, forest, and chaparral communities (Jameson 1951, Quast 1954, Lawrence 1966, Spevak 1983, Fellers and Arnold 1988, Wirtz et al. 1988) (also see table 10C). On the other hand, numbers of other species of white-footed mice in lower-elevation mixed-conifer, ponderosa pine, oak-pine woodland, and various hardwood and chaparral communities would be reduced or eliminated by clearcutting, brush removal, or fire. Management that promotes increased abundance of oaks would increase numbers of brush mice. In the San Gabriel Mountains, in mixed-chaparral communities on the San Dimas Experimental Forest, brush mice were rare on plots in chaparral that had not been burned for 28 years, but increased in abundance after burns. Brush mice increased to six times their preburn density on areas with normal burns and 14 times on areas with hot burns. Brush mice recolonized burned areas sooner than California mice (Wirtz et al. 1988). In coastal northern California (Hopland Field Station, Univ. of California), both brush and pinyon mice were adversely affected by converting chaparral to grassland, but positively affected by converting old, decadent chaparral to young- and intermediate-aged stands (Longhurst 1978). California mice were the only common *Peromyscus* in the mature montane chaparral at San Dimas Experimental Forest. They were the slowest of the white-footed mice to recolonize mixed montane-chaparral communities in the San Gabriel Mountains after burns. Captures after bums were greater on normal burns than hot burns, and postfire densities were generally greater than preburn densities (Wirtz et al. 1988). Management that promotes increased cover and vertical complexity of chaparral and woodlands, increased abundance of California-laurel and dusky-footed woodrats, and increased numbers of potential nests would enhance populations of California mice.

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