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Habitat Preferences and Distribution of Mammals in California Chaparral

Ronald D. Quinn

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Forty-nine species of mammals regularly occur in California chaparral, but none lives only in chaparral. Among the 49 species, 7 are found primarily in mature chaparral, 9 in young chaparral or along ecotones between chaparral and other plant communities, and 19 in riparian areas. Five species occur in many habitats but prefer chaparral in California, and 9 have wide ranges that encompass many communities including chaparral. By altering the structure of the plant community, fire in chaparral is important in determining the distribution and abundance of mammalian populations. Fire is not permanently destructive to the mammalian fauna. Wildlife habitat can be optimized by maintaining chaparral in many age classes, by restricting fuel reduction treatments to 1 to 100 ha, by protecting all trees, and by enhancing water sources. A given area of chaparral contains two to four common, and two to nine total, species of rodents. Seeds, fruits, and young vegetative growth are the most important plant foods in chaparral. Only 12 species of mammals are endemic to chaparral, because of the limited opportunity in both time and space for speciation to occur. Only kangaroo rats *(Dipodomys)* and chipmunks *(Eutamias)* have speciated in chaparral.

Retrieval Terms: wildlife, fire, plant community, ecology, California

The Author:

Ronald D. Quinn is a professor of biological sciences at California State Polytechnic University, Pomona, California, and a Station cooperator. This paper was presented at the Symposium on the Classification and Distribution of California Chaparral Ecosystems, held in conjunction with the 60th Annual Meeting, Western Society of Naturalists, December 28, 1979, Pomona. It has since then been revised and updated.

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This first systematic review of all species of mammals inhabiting California chaparral responds to a growing interest in the understanding and management of chaparral ecosystems.

Forty-nine species of mammals regularly occur in California chaparral, but none lives only in chaparral. Among the 49 species, 7 species (6 rodents and 1 rabbit) are found primarily in mature chaparral, 9 species (the mule deer and 9 rodents, including 5 kangaroo rats) in young chaparral or along ecotones between chaparral and other plant communities, and 19 species (12 bats and 7 terrestrial species) in riparian areas. Five species occur in many habitats but prefer chaparral in California, and nine other species have wide ranges that encompass many communities, including chaparral.

An area of chaparral (0.5 to 6.8 ha) generally contains two to four common, and two to nine total, species of rodents. Seeds, fruits, and young vegetation growth are the most important plant foods in chaparral.

Fire affects the distribution and abundance of mammalian populations in chaparral by altering the structure of the plant community and the availability of many foods. Fire does not permanently destroy the mammalian community. Patches of unburned chaparral serve as refugia and centers of dispersal for mammalian populations colonizing burns. Mammal population densities and distributions shift in response to the mosaic of plant age classes created by fires, and to the network of ecotones between classes. Between fires the abundances of rodent species change as each responds to its particular habitat requirements against the background of a changing plant community.

Management of the vegetation affects the presence and abundances of mammalian species. Wildlife habitat can be optimized for the community as a whole by maintaining chaparral in many age classes, by confining fuel reduction treatments to 1 to 100 ha, by protecting all native trees, and by protecting and enhancing all sources of surface water.

INTRODUCTION

California chaparral is composed of several plant associations found from the Oregon border on the north to northern Baja California on the south, occurring from near sea level to about 3000 m (Hanes 1977, 1981). In this paper the term "chaparral" refers only to the community of evergreen woody shrubs of the hills and the lower mountain slopes of California and northern Baja California. Despite the great geographical and floral diversity of chaparral, relatively few species of mammals are found in any given location and fewer still are classified as exclusive chaparral inhabitants.

Forty-nine species of mammals regularly occur in California chaparral, but none lives only in chaparral. Among the 49 species, 7 are found primarily in mature chaparral, 9 in young chaparral or along ecotones between chaparral and other plant communities, and 19 in riparian areas. Five species occur in many habitats but prefer chaparral in California, and 9 have wide ranges that encompass many communities including chaparral.

Although interest in the mammals of the California chaparral has grown, much of this interest has focused on only a few species. For example, a great deal has been written about the ecology and management of deer *(Odocoileus hemionus)* in chaparral (Dasmann 1962; Dixon 1934; Taber and Dasmann 1958; also see Urness 1981, and Wallmo and others 1981 for recent reviews). In recent years several researchers have investigated the rodents of chaparral as a convenient vehicle for studying general questions of community organization (Bradford 1976; Carnes 1978; Glanz 1977; Lubina 1978; Meserve 1976b, 1977; Nicholson 1978; Quinn 1979; Spevak 1983). A systematic review of all 49 mammalian species that occur in chaparral, however, has been lacking.

This paper describes each species or group of the 49 mammalian species, emphasizing their distributions and habitat preferences within chaparral in California, reviews the importance of fire and management activities to mammalian species, and outlines the structure of mammalian communities in chaparral.

In most cases mammals living in chaparral respond to the structure of the plant community, rather than to the presence of particular species of plants (Bayless 1980; Carnes 1978; Nicholson 1978). Habitat preferences of chaparral mammals are therefore described in terms of the age of the plant community, the amount of plant cover, proximity to openings, ecotones, and physical features such as rocky slopes, not in terms of a particular species of plant.

HABITAT PREFERENCES OF CHAPARRAL MAMMALS

Mature Chaparral

Mature chaparral contains shrubs, 1 to 3 m in height, that provide dense vegetative cover of 50 to 100 percent for wildlife. The first seven species of mammals listed in *table 1*, six rodents and one lagomorph, are found in mature chaparral, but are uncommon or absent in other habitats.

The brush rabbit *(Sylvilagus bachmani)* is a wary species that uses mature chaparral for cover, and feeds in openings near shrubs. In California the range of this species is congruent with the California chaparral.

The California pocket mouse *(Perognathus californicus)* is found only in chaparral and associated plant communities. The occurrence of this species appears to be spotty, and population densities are variable (Tucker 1966, Wirtz 1977). Some studies in young chaparral have shown pocket mice to be rare members of the rodent community (Carnes 1978; Quinn 1979). On the other hand, Wirtz (1977, 1981) found that this species comprised as much as 50 to 61 percent of all small mammal captures in both mature and recently burned chaparral. The California pocket mouse prefers edges between chaparral and other plant communities (Bradford 1976; Tucker 1966). Nicholson (1978) captured them in both ecotones and chaparral, while others have found none at all in chaparral (Bayless 1980; Tucker 1966).

Three of the 11 species of chipmunks living in California are chaparral dwellers. Two of these inhabit mature chaparral and replace one another at latitudinal boundaries. Merriam's chipmunk *(Eutamias merriami)* is found from the foothills of southern California through the Coast Ranges north to San Francisco Bay, and in the western foothills of the southern and central Sierra Nevada Mountains. It is replaced by the Sonoma chipmunk *(Eutamias sonomae)* in the chaparral of northern California. The obscure chipmunk *(Eutamias obscurus)* is parapatric with Merriam's chipmunk in the Transverse and Peninsular Ranges of southern California and Baja California (Callahan 1977).

One species of *Peromyscus*, the California mouse *(Peromyscus californicus)*, is specialized for life in the dense cover of heavy chaparral (Merritt 1978). Its range is restricted to dense

chaparral and associated woodlands of California and northern Baja California. It is a partially arboreal mammal (Bayless 1980, Meserve 1977) that specializes in eating flowers and seeds of shrubs and trees (McCabe and Blanchard 1950; Merritt 1974; Meserve 1976a). Of the many species of *Peromyscus*, it has the largest body size. The brush mouse *(Peromyscus boylii)*, as the common name implies, also prefers habitats with shrub cover (Carnes 1978; Holbrook 1978; Jameson 1952; Storer and others 1944). Nicholson (1978) suggested that the California mouse is socially dominant over the brush mouse, excluding it from areas where it would otherwise occur. This suggestion is supported by the observation of Vaughn (1954) that these two species are not microsympatric. By contrast, through radiotelemetry I have found both species utilizing the same shrubs on the same night.

The dusky-footed wood rat *(Neotoma fuscipes)* is one of the few species of mammals that flourishes in old, dense chaparral. The tall shrubs serve as a framework for its stick houses (Horton and Wright 1944; Linsdale and Tevis 1951), and provide cover and many pathways for arboreal foraging (Cranford 1977). Meserve (1974) found that this species is a food generalist, utilizing many plant foods. Enormous quantities of food are sometimes stored in its nests (Horton and Wright 1944).

Disturbed or Open Chaparral

A second category of mammals includes eight species of rodents and one artiodactyl (*table 1*, species 8 to 16). These species are common in chaparral with less than 50 percent vegetative shrub cover. Such animals favor the open shrubland created by fire and other disturbances in chaparral. They may, however, require proximity to mature chaparral (Ashcraft 1979; Bradford 1976; Nicholson 1978).

Of 13 species of kangaroo rats that occur in California, 5 inhabit chaparral. Three of these have extensive ranges that divide chaparral by latitude. The Pacific kangaroo rat *(Dipodomys agilis)* is the southernmost species, found between Baja California and the Transverse Mountain Ranges of southern California. It is replaced by the Heermann kangaroo rat *(Dipodomys heermanni)* in the southern Sierra Nevada foothills and coastal mountains of Santa Barbara County. The range of *D. heermanni* extends north to the central Sierras and through the Coast Ranges to San Francisco Bay. This species is replaced in turn by the California kangaroo rat *(Dipodomys californicus)* in northern California and the brush fields of southwestern Oregon. These three species are quite similar in general appearance, body size, and behavior. Field studies of the Heermann and Pacific kangaroo rats suggest that they are ecological equivalents (Quinn 1979). Both species construct burrows, take dust baths, and forage in the openings between chaparral shrubs. They are most abundant in the open plant community that occurs 2 to 5 years after a fire, but smaller numbers of individuals can be found in the more limited openings of mature chaparral.

The Santa Cruz kangaroo rat *(Dipodomys venustus)* is found in the Coast Ranges between northern San Luis Obispo County and San Francisco Bay. The big-eared kangaroo rat *(Dipodomys elephantinus)* is known only from the southern portion of the

Table 1—*Habitat preferences of terrestrial mammals in the California chaparral*

Species	Mature chaparral	Open chaparral	Riparian	Many plant communities
1. Brush rabbit *(Sylvilagus bachmani)*	✱	✚		
2. Merriam's chipmunk *(Eutamias merriami)*	✱			
3. Obscure chipmunk *(Eutamias obscurus)*	✱			
4. Sonoma chipmunk *(Eutamias sonomae)*	✱			
5. California pocket mouse *(Perognathus californicus)*	✱	✚		
6. California mouse *(Peromyscus californicus)*	✱			
7. Dusky-footed wood rat *(Neotoma fuscipes)*	✱			
8. Pacific kangaroo rat *(Dipodomys agilis)*	✱	✱		
9. Heermann kangaroo rat *(Dipodomys heermanni)*	✱	✱		
10. California kangaroo rat *(Dipodomys californicus)*	✱	✱		
11. Santa Cruz kangaroo rat *(Dipodomys venustus)*	✱	✱		
12. Big-eared kangaroo rat *(Dipodomys elephantinus)*	✱	✱		
13. California ground squirrel *(Spermophilus beecheyi)*		✱	✚	✱
14. Cactus mouse *(Peromyscus eremicus)*		✱		✱
15. Desert wood rat *(Neotoma lepida)*	✚	✱		✱
16. Mule deer *(Odocoileus hemionus)*	✚	✱	✚	✚
17. Common opossum *(Didelphius marsupialis)*			✱	✚
18. Ornate shrew *(Sorex ornatus)*			✱	✚
19. Vagrant shrew *(Sorex vagrans)*			✱	✚

✱ = common
✚ = occasional

continued

Table 1—*Habitat preferences of terrestrial mammals in the California chaparral (continued)*

Species	Mature chaparral	Open chaparral	Riparian	Many plant communities
20. Harvest mouse *(Reithrodontomys megalotis)*		✚	✱	✱
21. Striped skunk *(Mephitis mephitis)*			✱	✚
22. Raccoon *(Procyon lotor)*			✱	✚
23. Ringtail *(Bassariscus astutus)*			✱	✚
24. Brush mouse *(Peromyscus boylii)*	✱	✚		
25. Audubon cottontail *(Sylvilagus audubonii)*	✱	✱		✱
26. Gray fox *(Urocyon cinereoargentus)*	✱	✚	✚	✚
27. Spotted skunk *(Spilogale gracilis)*	✱	✱		✱
28. Wild boar *(Sus scrofa)*	✱	✚	✱	
29. Botta pocket gopher *(Thomomys bottae)*	✚	✱	✱	✱
30. Deer mouse *(Peromyscus maniculatus)*	✚	✱	✚	✚
31. Pinyon mouse *(Peromyscus truei)*		✱	✱	✱
32. Coyote *(Canis latrans)*	✚	✱	✚	✱
33. Black bear *(Ursus americanus)*	✱	✚	✚	✱
34. Long-tailed weasel *(Mustela frenata)*	✚	✚	✱	✱
35. Badger *(Taxidea taxus)*		✚	✚	✱
36. Bobcat *(Lynx rufus)*	✱	✱	✚	✱
37. Mountain lion *(Felis concolor)*	✚	✱	✚	✱

✱ = common
✚ = occasional

Gabilan Mountains in Monterey and San Benito counties. From the limited information published on these two species (Bradford 1976; Grinnell 1922), they seem to be ecologically similar to the Heermann and Pacific kangaroo rats.

In chaparral the California ground squirrel *(Spermophilus beecheyi)* is most numerous near disturbances such as roadsides, old buildings, dumps, agricultural fields, and fuelbreaks. Ground squirrels did not occur in the extensive unbroken chaparral of the central Santa Ana Mountains until roads provided avenues for colonization from the foothills (Pequegnat 1951).

The cactus mouse *(Peromyscus eremicus)* occurs across the deserts of western North America. This species was found in moderate numbers during the first 4 years after a chaparral fire in the Santa Margarita Mountains of Riverside County *(fig. 1)*. During those years the structure of the plant community was similar to that of desert scrub.

The desert wood rat *(Neotoma lepida)* is found in a variety of arid and subarid plant communities. In chaparral it occurs in rocky, relatively open habitats (Carnes 1978; McHenry 1965; Nicholson 1978; Quinn 1979), and in recently burned areas (Carnes 1978; Quinn 1979; Spevak 1983). This species can locally specialize on specific food plants, such as certain species of prickly pear *(Opuntia)* and sage *(Salvia)*, that are relatively unpalatable to most other herbivores (Macmillen 1964; Meserve 1974). Since desert wood rats often construct their nests beneath and between rocks and boulders, the presence of this species in chaparral and elsewhere is associated with rock outcrops (Thompson 1982).

Deers *(Odocoileus hemionus)* are found in all California chaparral, although population densities vary greatly with space and time (Dasmann 1962). The Columbian black-tailed deer *(O. h. hemionus)* occurs in the chaparral of northern California; the California mule deer *(O. h. californicus)* is found in the Central Coast Ranges and the western Sierra Nevada Mountains, south to Los Angeles County; and the southern mule deer *(O. h. fuliginatus)* lives in the chaparral of Orange, Riverside, and San Diego counties. The wide differences in population densities of chaparral deer are caused by three variables: cover, forage, and water. The quality of both forage and cover is a function of fire patterns (Ashcraft 1979). During the first year after a large chaparral fire, deer populations in the fire area are reduced by displacement of individuals and lack of forage. In the second and third years after fire, the deer population increases due to the growth of succulent forage in the recovering plant community (Biswell 1961; Taber and Dasmann 1958). This increase is temporary, and it is confined to areas within 90 m of the cover provided by older chaparral. Summer and fall, when moisture and protein content of chaparral shrubs declines to the lowest seasonal levels, are the most critical times for deer populations (Urness 1981). At these times activities of deer are confined to areas within 0.8 to 1.2 km of freestanding water. A much smaller part of southern than northern California is classified as prime deer habitat (McLean 1940). This lack of prime habitat may be due to the greater aridity of the southern part of the state.

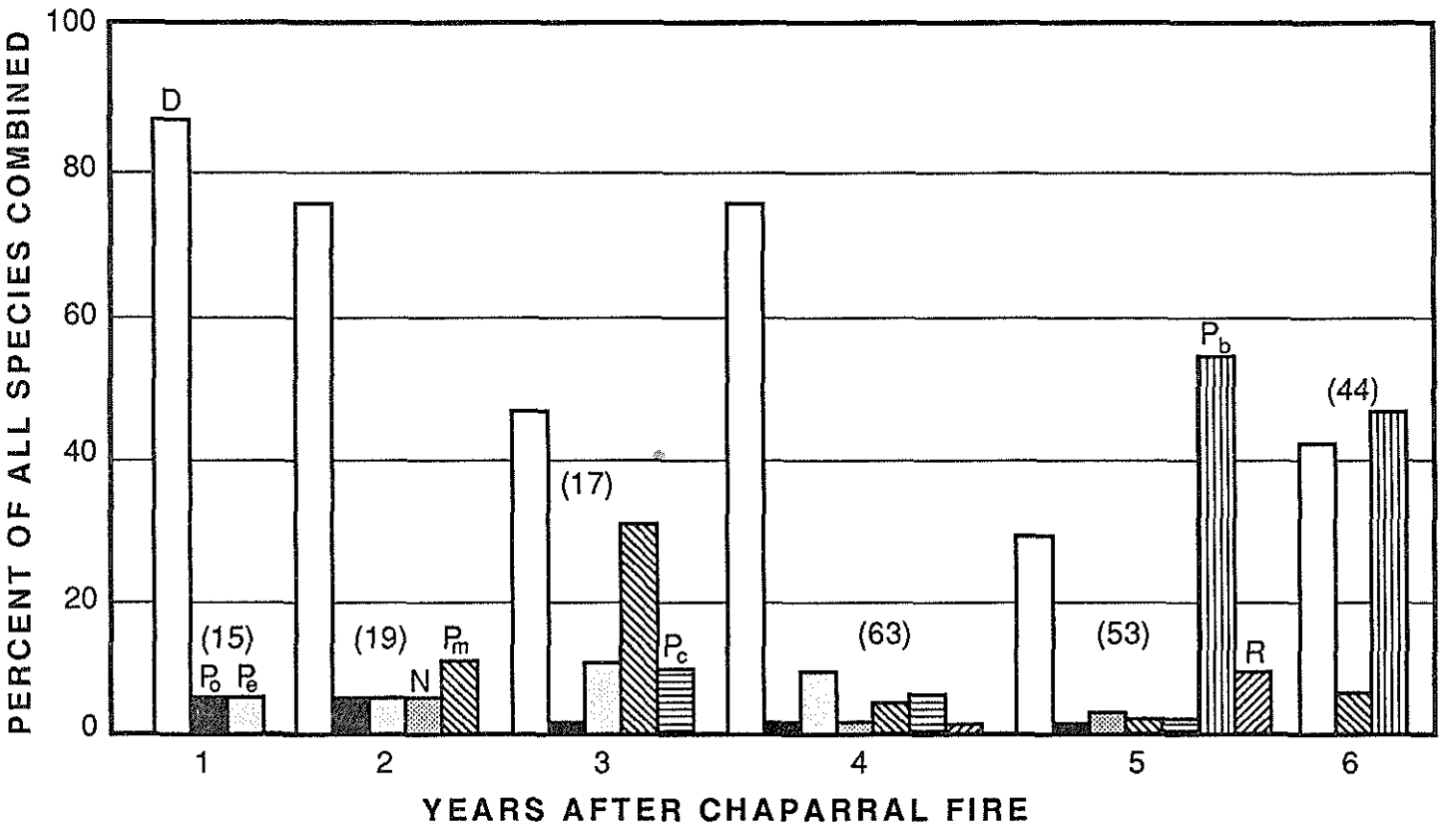

Figure 1—The composition of a chaparral rodent community changed 6 years after a wildfire. Population percentages are calculated from minimum population sizes for annual trapping seasons lasting 4 to 8 months. Figures in parentheses represent the total number of individuals of all species known alive on the day for which the population percentages were calculated. Species are: D = *Dipodomys agilis*, N = *Neotoma lepida*, P_b = *Peromyscus boylii*, P_c = *Peromyscus californicus*, P_e = *Peromyscus eremicus*, P_m = *Peromyscus maniculatus*, P_o = *Perognathus californicus*, R = *Reithrodontomys megalotis*.

Riparian Areas

Within chaparral communities there are seven species of terrestrial mammals that occur mainly in riparian habitats *(table 1*, species 17 to 23). These habitats occur almost exclusively in canyon bottoms and consist of ribbons of trees, grasses, and other mesic vegetation along watercourses. They sometimes include surface water, deep and loose soil, and other environmental variables associated with the physical processes that take place in canyons with flowing water. As wildlife habitats these areas have little in common with chaparral. The justification for classifying such species as chaparral animals is a matter of juxtaposition, since the home ranges of riparian mammals are adjacent to, and may even include, nearby chaparral.

The vagrant shrew *(Sorex vagrans)* and the ornate shrew *(Sorex ornatus)* are reported from the canyons of chaparral areas in northern and southern California, respectively. Both species prefer the moist soil and protective cover afforded by streamside habitats. I have unintentionally captured vagrant shrews away from canyons in live traps set for rodents under coast live oak trees *(Quercus agrifolia)*. They were undoubtedly searching for invertebrates in the thick leaf litter beneath these trees.

The harvest mouse *(Reithrodontomys megalotis)*, although found in many areas in California, is most numerous in thick grasses and forbs near water. It uses such thickets for nesting and foraging. In chaparral it has been live-trapped in low frequencies at places with dense grasses and forbs, such as post-fire communities and fuelbreaks, as well as in relatively mesic areas with oaks and other trees (Blong and others 1978; Carnes 1978; Nicholson 1978; Quinn 1979; Stavert 1976).

The opossum *(Didelphius marsupialis)* is an introduced species that has become naturalized in some chaparral areas. It was brought to California early in the twentieth century and is now common in mountain canyons below 1200 m (Grinnell and others 1937). These mammals avoid the dense growth of mature chaparral, and are not found more than 3.2 km from surface water (Grinnell and others 1937, Verts 1967).

Raccoons *(Procyon lotor)* are omnivorous, highly opportunistic mammals found in many habitats, including chaparral. They must, however, be close enough to water for regular visits. In most chaparral areas this restricts their ranges to larger canyon drainages with permanent surface water.

Relatively little is known about the biology of the ringtail *(Bassariscus astutus)*. Although its range includes the entire state, it is absent from many areas. It shows a distinct preference for canyons and rocky slopes, especially chaparral between 600

and 1000 m (Grinnell and others 1937). Hall (1946) reports that it does not occur more than 0.4 km from surface water, but Stager (1953) found ringtails in desert mountain ranges with no surface water. In chaparral areas the preference of this animal for dense brush, rocky slopes, and perhaps nearby water probably confines the ringtail to canyons and adjacent slopes.

Bats are difficult to classify according to habitat preferences when categories are based on plant communities. The most important resources for most species of bats are adequate roosting sites and watering areas. Feeding occurs above the vegetation, and foraging patterns are most responsive to the distribution of insect prey. Bats are included here with riparian mammals because most species forage over or near water. Of 24 species of bats that regularly occur in California, half are classified here as chaparral mammals. The following species forage over the water and riparian vegetation of canyons in chaparral:

Myotis thysanodes	(fringed myotis)
Myotis yumanensis	(Yuma myotis)
Myotis californicus	(California myotis)
Myotis subulatus	(small-footed myotis)
Myotis evotis	(long-eared myotis)
Myotis volans	(hairy-winged myotis)
Myotis lucifugus	(little brown myotis)

The species of bats listed below are found in many habitats, including chaparral:

Tadarida braziliensis	(Mexican free-tailed bat)
Eptesicus fuscus	(big brown bat)
Antrozus pallidus	(pallid bat)
Pipistrellus hesperus	(canyon bat)
Plecotus towndsendii	(big-eared bat)

Widespread Chaparral Species

In California five species of mammals are most abundant within chaparral, while having ranges that extend well beyond the borders of the state (*table 1*, species 24 to 28). All of these species flourish in dense brush.

The brush mouse *(Peromyscus boylii)* prefers habitats with dense shrub cover (Holbrook 1978; Jameson 1952; Storer and others 1944). Although it is rarely trapped in the relatively open chaparral of south slopes (Nicholson 1978), and occurs in low numbers in young chaparral for the first 3 years after fire (Quinn 1979), it does utilize microhabitats with less vegetative cover than the California mouse. Nicholson (1978) concluded that in areas where the brush mouse and California mouse occur together, the brush mouse is excluded from the most dense cover by the socially dominant California mouse. The widespread brush mouse is commonly associated with trees in other parts of western North America (Holbrook 1978; Jameson 1952; Matson 1974). Blong and others (1978), when trapping in six chaparral plant communities, found the brush mouse to be the most abundant species of rodent in coast live oak, black oak *(Quercus kelloggii)*, and riparian associations. Each of these plant communities has an overstory of trees. This species is an excellent climber that is frequently caught in arboreal traps (Matson 1974). In live-trapping in mature, north slope chaparral, with equal numbers of arboreal and ground traps, I found that 34 percent of all brush mouse captures were above the surface of the ground. Radiotracking in mixed chaparral showed that the movements of this species were mostly above the ground in shrubs.

The cottontail rabbit *(Sylvilagus audubonii)* is found in many plant communities throughout the western United States. In chaparral this animal uses dense brush for cover and nesting (Fitch 1947). The habit of feeding in openings near cover excludes this species from chaparral with a continuous overstory of shrubs. There is evidence that concentrated grazing activity by cottontail and brush rabbits is responsible, at least in part, for a "bare zone" located at chaparral-grass ecotones which lacks any large plants (Bartholomew 1970; Halligan 1973).

The mobility, adaptability, and broad diet of two species of mammalian carnivores, the gray fox *(Urocyon cinereoargentus)* and the western spotted skunk *(Spilogale gracilis)*, allow them to exist in many habitats. In California, however, they are most abundant in chaparral. The gray fox, although found everywhere in the state, is most common in mature chaparral at elevations of 300-900 m (Grinnell and others 1937) where it frequents canyons, rocky places, and woodlands. This animal moves easily through dense brush and regularly climbs into trees and large shrubs. Although the gray fox must have surface water for drinking, its large home range of 120 ha (Fuller 1978) and mobility permit it to hunt far from the watered canyons. Its diet in chaparral probably consists mainly of rodents, although it eats many other animals and plants as well. The western spotted skunk is found on rocky slopes in foothill areas of California. Within these areas it is most common in lower elevation chaparral and coastal sage scrub (Grinnell and others 1937).

Several decades ago European wild pigs *(Sus scrofa)* were introduced into California in Monterey County and the foothills of the Sierra Nevada Mountains (Pine and Gerdes 1973). Populations of this species have since naturalized and extended their range in several areas, and some have hybridized with escaped domestic pigs. During the 1950's the California Department of Fish and Game transplanted some of these feral pigs to new areas. Chaparral appears to be prime habitat for these animals, as long as surface water and abundant acorns are available (Pine and Gerdes 1973).

Species Occurring in Many Habitats

Some species of mammals occur in many habitats, both in California and elsewhere (*table 1*, species 29 to 37). Although they are found in chaparral, and may be important components of the fauna, these species are usually equally or more abundant in other communities. This group of mammals includes four rodent and five carnivore species.

Botta pocket gophers *(Thomomys bottae)* have often been

described as responding to soil quality, with the highest population densities in deep or grassland soils (Howard and Childs 1959; Proctor and Whitten 1971; Vaughn and Hansen 1964). Although these preferences would seem to make the generally shallow, rocky soils of chaparral a suboptimal habitat at best, pocket gophers are found in many chaparral areas. I have found them to be especially numerous during the first 3 years after fire, when the abundance and diversity of herbaceous plant foods is greatest. This observation is consistent with that of Best (1973), who reported pocket gophers to be more abundant in disturbed areas than in places with mature vegetation. Pocket gopher mounds are frequently seen in ecotones between chaparral and grasslands.

The ubiquitous deer mouse *(Peromyscus maniculatus)* is undoubtedly the most adaptable rodent in North America. It is found in widely varying abundances in all chaparral communities. This opportunistic species reproduces rapidly after various kinds of environmental disturbances, or when other species of rodents have been eliminated (Holbrook 1978). The deer mouse forages only on the ground, not in shrubs as do other species of *Peromyscus* that inhabit chaparral (Holbrook 1978; Meserve 1977). Given these characteristics it is not surprising that this animal flourishes from the second to fourth years following a chaparral fire, when open ground is present and populations of other species of *Peromyscus* have been temporarily reduced or eliminated (Blong and others 1978; Carnes 1978; Quinn 1979; Wirtz 1977). Deer mice can be the second most abundant species of rodent, after kangaroo rats, during the third year after a fire *(fig. 1)*. Blong and others (1978) found them to be the most abundant species of rodent in interior live oak woodland *(Quercus wislizenii)* 4 years after fire. They also found deer mice to be rare in plant communities dominated by trees. Around mature chaparral this species is captured more frequently at ecotones between the shrub community and adjacent grasslands than within the chaparral, where it is rare (Nicholson 1978, Wirtz 1977). Deer mice are sometimes the most common species of rodent following mechanical disturbance of the chaparral (Carnes 1978; Quinn 1983).

The pinyon mouse *(Peromyscus truei)* is found throughout most of California, and across other parts of the southwestern United States, in places where some tree or heavy shrub cover is available (Bradford 1976; Carnes 1978; Holbrook 1978; Lawrence 1966; McCabe and Blanchard 1950; Nicholson 1978). It is often found in mature chaparral, where it may be one of the most abundant species of small mammal (Bradford 1976; Carnes 1978). The pinyon mouse does not occur on the coastal side of the mountains of southern California, where it is replaced by the brush mouse. The brush mouse and pinyon mouse apparently compete in chaparral areas where the two species are sympatric (Nicholson 1978). Bradford (1974) found that in chaparral the pinyon mouse experiences water stress in summer and early fall. This stress is relieved in the fall when acorns become available as a source of metabolic water.

The highly versatile coyote *(Canis latrans)* is found in most of the ecosystems of western North America, including chaparral. The steep slopes and heavy cover of most chaparral communities impede its movements. Ecotones, fuelbreaks, roads, trails, and open chaparral are frequented more by this animal than dense, unbroken cover. In southern California, where chaparral is adjacent to urban areas, coyotes forage at night along the urban fringe and return during the day to the cover of chaparral.

The black bear *(Ursus americanus)* is found in the chaparral of northern California, the Sierra Nevada Mountains, and in the Tehachapi Mountains and Coast Ranges where it has extended its range since the local extinction of the grizzly bear *(Ursus arctos)*. It also occurs in the San Bernardino and San Gabriel Mountains of southern California, where it was introduced in 1933 (Burghduff 1935). Black bears tend to prefer oak woodland and forests over chaparral, but they do make extensive use of chaparral in southern California for cover and for feeding on preferred plant foods (Boyer 1976; Novick 1979).

All of the California chaparral was once occupied by the California grizzly bear. In northern California and the Sierra Nevada Mountains black and grizzly bears coexisted. In the Coast Ranges south of San Francisco Bay and the mountains of southern California, however, the grizzly was the only species of bear. It was more adaptable than the black bear, consuming many food items and occupying many habitats from the high mountains to coastal beaches (Storer and Tevis 1955). Chaparral was used by the grizzly bear for escape and resting, and prominent bear trails existed beneath the canopy of dense chaparral thickets. This animal consumed the fruits of chaparral shrubs, and acorns from the oaks. Their predilection for manzanita fruits is reflected in the generic name of this group of shrubs, *Arctostaphylos*, which means "bearberry."

The long-tailed weasel *(Mustela frenata)* occurs in any terrestrial habitat with sufficient prey populations of small mammals (Hall 1951). In most chaparral areas its need for surface water, and limited movement range of 40-75 m (Glover 1943), probably combine to restrict its occurrence to the immediate vicinity of canyons.

The wide-ranging badger *(Taxidea taxus)* is found everywhere in California. In chaparral it is most common where the vegetation is sparse due to fire or other disturbance, and where there are large populations of burrowing rodents such as California ground squirrels or kangaroo rats (Grinnell and others 1937).

The bobcat *(Lynx rufus)* is most common in canyons and on rocky slopes having sufficient shrub cover. Chaparral shrubs permit concealment while stalking. Population densities of bobcats as high as 10 per square kilometer have been measured in the chaparral of San Diego County.

Although found in many habitats the mountain lion *(Felis concolor)* is most abundant where deer, its main prey, are numerous. In chaparral, therefore, mountain lions would be attracted to the edges of recent burns where deer tend to congregate (Biswell 1961; Taber and Dasmann 1958).

Fire

The most important factors in the distribution and abundance of mammalian species within chaparral are the direct and indi-

rect effects of fire. Intense wildfires temporarily drive away large mammals (Chew and others 1959) and destroy many small mammals that take refuge in flammable nests above the ground (Quinn 1979). More importantly, fire drastically alters the structure of the plant community and sets into motion a sequence of physical and biological processes that affect the animal community for many years.

Fire does not permanently destroy the animal community (Cook 1959; Lawrence 1966; Longhurst 1978; Wirtz 1977, 1981). Mammalian species that live in the chaparral have coexisted with a fire cycle for at least 2 million years, since the development of a Mediterranean climate in California (Raven 1973). Therefore all species of plants and animals that live in this community must have ways to perpetuate or reestablish populations after fire. There is, however, no evidence that any species of mammal has adaptations that have evolved specifically for survival of chaparral fires. Larger species that can move quickly, such as deer and foxes, simply flee from the fire. Burrowing species, like kangaroo rats and species that will take refuge in burrows and other recesses beneath the ground, such as deer mice, can survive fires in underground shelters. Species that are physically and behaviorally incapable of escaping fire, such as brush rabbits and wood rats, are directly destroyed by the fire (Quinn 1979). From an evolutionary point of view, however, these deaths are inconsequential. Whether or not an individual animal or local population survives the direct effects of fire, the continued existence of all populations in the fire area is determined by the habitat created by the fire. Adult animals that are permanently displaced from their home ranges by fire, and are unable to establish themselves elsewhere, will die as surely as if they had been directly killed by the fire. Those animals that remain in the fire area and survive, or return immediately to it, must be able to live in the drastically altered habitat or they too will die.

Chaparral wildfires do not thoroughly or uniformly burn over large tracts of land because chaparral grows for the most part on hills or mountains, and because large fires are usually driven by gusty, erratic winds. The combination of shifting wind and broken terrain causes fires to burn with uneven intensity and direction, at times entirely skipping some places. The islands of unburned chaparral thus created, as well as unburned chaparral beyond the perimeter of the burn, serve as centers of dispersal for animal populations immigrating into the burned area.

As mammalian habitat, chaparral may be visualized as a mosaic. The major pieces of this mosaic are marked by the boundaries of individual fires, as they would appear on a map. Within these larger pieces there are smaller pieces delineated by islands of vegetation entirely skipped by fire, and pieces burned with varying intensities. The ecotones between such pieces are an essential aspect of this mosaic. These ecotones are used heavily by mammals such as deer and rabbits that take advantage of the unburned brush as cover and adjacent open areas for feeding (Bell 1974; Bell and Studinski 1972; Bradford 1976; Carnes 1978; Larson 1985; Stavert 1976). Predators in turn are attracted to these ecotones by the concentration of herbivorous prey populations.

Species of mammals respond to this mosaic of plant age classes, and to the network of ecotones between pieces, with shifting population densities and population centers. Many species of mammals that are abundant in recently burned chaparral will be rare or absent in chaparral that has not burned for 20 or more years. The opposite is also true. For example, young chaparral will have deer mice and coyotes, but no dusky-footed wood rats or California mice, while California mice and wood rats will be abundant in mature chaparral where deer mice and coyotes are lacking. Changes in relative abundances of the members of a rodent community were studied for 5 years after a chaparral wildfire *(fig. 1)*. The population changes in this community followed four patterns: (1) populations of four species (deer mouse, cactus mouse, California mouse, and harvest mouse) increased, decreased, and disappeared in a period of a few years; (2) when present, the California pocket mouse and the desert wood rat were always relatively rare; (3) the brush mouse occurred in large numbers only at the end of the study; and (4) the relative abundance of the Pacific kangaroo rat was high but variable throughout the study. Similar patterns of post-fire changes in the rodent community over a period of years have been observed by Wirtz (1981).

HABITAT MANAGEMENT

The structure of the chaparral plant community is sometimes changed deliberately to meet various management goals, including creation or improvement of wildlife habitat. Chaparral has been converted to grassland to reduce fuel accumulations, to improve rangelands, to provide access and safety for firefighting operations, and to increase water yields. Chaparral shrubs have been reduced or removed altogether by various combinations of fire, herbicides, and mechanical manipulations (Green 1977). Brush removal is frequently followed by planting of perennial or annual grasses. The goal is sometimes not to replace chaparral with other plant communities, but rather to keep selected brushlands young enough to avoid the fire hazard associated with the accumulation of fuels in older chaparral.

All of these alterations to the plant community have effects on the animal community in varying degrees. Numerous studies have shown that the presence and relative abundances of mammalian species are affected by manipulations by either fire, herbicides, or mechanical means (Bell 1974; Bell and Studinski 1972; Carnes 1978; Lillywhite 1977a, 1977b; Quinn 1979, 1983, 1986; Stavert 1976; Wirtz 1974, 1977, 1981). Conversion from chaparral to grass creates additional resources not only for some species of chaparral mammals, such as kangaroo rats, but also permits the existence of mammals that would otherwise be absent, such as California voles *(Microtus californicus)* and harvest mice (Bell and Studinski 1972; Blong and others 1978; Lillywhite 1977a, 1977b; Stavert 1976; Wirtz 1974, 1977,

1981). None of these manipulations is inherently desirable or undesirable for the wildlife community as a whole, because the changes that enhance some mammalian species may be detrimental to others.

To optimize chaparral habitat for all species of wildlife, I offer four recommendations. First, keep chaparral in a mixture of several age classes. In this way, whatever the stages of plant community development that are optimum for a particular species of mammal, those stages will be present. It is unnecessary to manage for chaparral habitats older than 20 to 30 years. By this age chaparral shrubs have reached their fullest structural development, and there is no evidence that any species of mammal will be benefited by allowing the plant community to grow older. For example, because of frequent fires, almost none of the many thousands of hectares of chaparral on the south face of the San Gabriel Mountains of southern California is older than 30 years, yet no species of mammal is known to be absent from this area because of the lack of older chaparral.

Second, if chaparral is maintained in young age classes by design, such as prescribed fire, then the size of the treated areas should be on the order of 1 to 100 ha, rather than the thousands of hectares that are consumed by larger wildfires. The home ranges of most mammalian species are small enough that populations can be supported inside areas of this size. Species with home ranges larger than the recommended treatment size, such as the bigger carnivores, will benefit by having a more heterogeneous habitat within their home ranges. This habitat diversity will provide these species with a wider range of food from which to select. A very important result of the creation of such a fine-grained habitat mosaic is the maximization of ecotones between age classes, and between chaparral and other plant communities. As pointed out earlier, these ecotones are important to several species of grazing and browsing mammals, and to the predators that feed upon them.

Third, any populations of native trees present in chaparral areas should be protected, and their growth encouraged. Trees are found in riparian areas and washes, on steep north and east slopes, in places with unusually deep soil, around springs, and at the upper elevational limits of chaparral where it intergrades with forests and woodlands. These trees provide shelter for a few arboreal and semiarboreal species of rodents including the western gray squirrel *(Scirus gresius)*, a species that otherwise would not be present. The mast crops of the trees are an additional source of food for wildfire. Some trees, such as the coast live oak *(Quercus agrifolia)*, have an understory of herbs and shrubs that serve as cover, browse, and fawning areas for mule deer.

Fourth, all sources of surface water should be protected and enhanced. Many mammalian species, classified here as riparian, have local distributions that are limited by proximity to water. These species will have their habitat extended by making water available in chaparral areas where it is now lacking, particularly in the rainless months of summer and fall.

COMMUNITY STRUCTURE

Evolution of Endemic Species

The opportunity, either in time or space, for mammalian species endemic to chaparral to evolve has been limited. The California chaparral is circumscribed by a Mediterranean climate which is quite recent, having first appeared during the Pleistocene Epoch (Raven 1973). Although California chaparral spans 12 degrees of latitude, and occurs in several distinct geographical areas, it has a scattered distribution within most of that range. Extensive unbroken tracts of chaparral are found only in the mountains of southern California. Chaparral covers only about 3.5 million ha, or 5 percent, of the State of California (Hanes 1977; Weislander and Gleason 1954).

The first 12 species listed in *table 1*, 11 rodents and one lagomorph, are endemic to chaparral. Compared to mammals as a whole, all of these species have relatively short generation times and large numbers of offspring. They also have limited mobility and thus are relatively easily separated into distinct populations by geographic barriers. These characteristics have enabled these animals to speciate in chaparral despite the limitations of time and space.

Five kangaroo rats (genus *Dipodomys)* have evolved in the California chaparral, and every chaparral area contains at least one such species. By the time the ancestors of these species had spread to California in the early to middle Pleistocene, a Mediterranean climate had already developed and chaparral quite likely was subject to periodic fires. The speciation of the genus was facilitated in three ways by preadaptation to the fire cycle: (1) kangaroo rats survive fires by remaining in their burrows (Quinn 1979); (2) their food resources, seeds and insects, are available after chaparral fires; (3) the open habitat created by the fire is ideal for their foraging activities.

Widespread Species

Most species of mammals that occupy chaparral are also found in other plant communities. Most of these species have ranges that extend far beyond the limits of chaparral. They have habitat preferences that include, but are not limited to, chaparral. They exist in chaparral because of the resources that it has in common with other communities, not because of its unique attributes. For example, dense shrubs intermixed with openings provide suitable habitat for cottontail rabbits, mule deer, and gray foxes. These species are therefore found in chaparral, coastal sage scrub, broken coniferous forest, and many other places with similar habitat structure. Deer mice and California ground squirrels are found in chaparral after it is disturbed by fire, but these species also occur in many other types of disturbed habitats.

Species Numbers and Population Densities

Investigators participating in the International Biological Program (IBP) studied the small mammal fauna in the chaparral of San Diego County in each season for 2 years (Cody and others 1977; Glanz 1977). They confined their analysis to rodents, since larger mammals were present in densities too low to facilitate comparisons between sites. Cody and others (1977) reported 2 to 4 common species of rodents, and 2 to 9 total species from 19 trapping grids of 0.5 ha each. Glanz (1977) listed 5 common species and 13 total species for all grids combined. Trapping in nearby montane forests resulted in fewer common (3) and total (9) species of rodents. Coastal sage scrub, on the other hand, had more common species of rodents (8) and consistently higher overall population densities than chaparral. In the chaparral of northern San Diego County, I found five common and eight total species of rodents in 5 years of sampling on a 6.8-ha site *(fig. 1)*. In the IBP studies, combined population densities of all species of small mammals ranged from 3.0 to 44.0 per hectare at four selected sites. On a single site, a sandy ravine, combined population densities ranged from 8 per hectare in the spring to 44 per hectare 1 year later.

Plant Foods

Chaparral produces large seasonal crops of seeds and fruits. In mature chaparral, these seeds and fruits are produced by the shrubs. Some, such as manzanita *(Arctostaphylos)* and various species of *Prunus*, are favored by mammalian herbivores. For the first 2 to 5 years after fire, short-lived herbaceous and suffrutescent plants generate a large and diverse crop of seeds. These fruits and seeds are an important component in the diet of many rodents (Glanz 1977, Meserve 1976a) and probably account, in part, for the fact that 50 percent of the mammalian species found in chaparral are rodents. Foliage of the mature shrubs is sclerophyllous, and many plant species have leaves laden with oils, terpenes, and other unpalatable secondary plant substances (Hanes 1977). Consequently the vegetative parts of some mature chaparral shrubs are regularly browsed by only a few species of mammals, such as the dusky-footed wood rat and the mule deer. Mature chaparral is largely devoid of an herbaceous understory, and affords little food for grazing herbivores. Most herbaceous growth and the tender crown sprouts of young chaparral, on the other hand, are important sources of food for herbivorous mammals such as rabbits, mule deer, and rodents.

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