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Abstract.—Wildfires in southern California chaparral burn at high intensities and often cover thousands of hectares. Some small mammals survive the fire, while others colonize from scattered unburned islands and from intact vegetation bordering the main fire perimeter. For ten years (2002–2011) we live-trapped two grids and used the number of captures to examine post-fire small mammal use of a narrow 65-m zone straddling the high-contrast edge between burned and unburned chaparral on the perimeter of a high-intensity wildfire. Results indicate that agile kangaroo rats (*Dipodomys agilis*) were captured more often in open, burned areas than in unburned chaparral. Deer mice (*Peromyscus maniculatus*) were captured equally in burned and unburned chaparral but did not show an affinity for either habitat or the edge of the burn. Pinyon mice (*Peromyscus truei*) were captured most often in unburned chaparral throughout the study but were prevalent on the burn edge in years one and four. In the first year post-fire, California mice (*Peromyscus californicus*) were captured more frequently in unburned than burned chaparral but in years four and five, captures shifted toward the edge and then into the burn areas in year nine. We did not find evidence that any of the four species were dedicated edge specialists in this study. Neither pinyon mice nor California mice appeared to be permanent residents of the burns in the first ten years post-fire. We suggest that future research on post-fire small mammal succession in chaparral would benefit from chronosequence studies that give a more comprehensive, long term picture of succession.

Introduction

Chaparral wildfires in southern California, especially those driven by hot, dry Santa Ana winds in the fall, spread quickly, burn at high intensities, and have the potential to reach thousands of hectares in size. Post-fire temporal and spatial patterns of burn-area re-colonization by small mammals depend on a several factors, but primarily on the number of animals surviving the fire *in situ* (Banks et al., 2011) and on animals re-entering the burn from refugia (*e.g.*, unburned brush, rock outcrops, riparian zones). Since chaparral fires usually do not leave vegetation mosaics, unburned islands within large (thousands of hectares) burns often are few in number, vary greatly in size, and tend to be widely scattered (Quinn 1990; Borchert et al., 2003). Compared to unburned islands, intact chaparral bordering the fire perimeter offers a more dependable source of colonists and is more likely to harbor the full contingent of small mammal species, and in greater numbers, than vegetation islands (Longland and Bateman, 2002).

Management strategies for conserving faunal diversity after wildfires depend on a multi-scale understanding of fire effects (Di Stefano et al., 2010). The earliest post-fire

small mammal studies in chaparral focused on the colonization of individual sites in burned and unburned chaparral (Lawrence 1966; Wirtz 1977; Wirtz et al., 1988; Wirtz 1995). Often, however, proximity of burn trapping grids to the nearest unburned refugia was not stated and it was assumed that the rate of re-occupation was not dispersal-limited (Rosario and Mathias, 2007). More recently, research on small mammal succession has shifted to much larger scales (Schwilk and Keeley, 1998; van der Ree and Loyn, 2002; Brehme et al., 2011; Diffendorfer et al., 2012). Trapping grids in these studies were placed in both unburned vegetation as well as in the burned area at varying distances from known refugia. Results of these studies have provided a more complete picture of the considerable variability in small mammal re-colonization that can occur at the landscape scale.

A conspicuous feature of all chaparral wildfires is the high-contrast, hard edge along the burn perimeter and at the margins of unburned islands. While there is extensive literature on the effects of edges on small mammals in unburned habitats (e.g., Murcia 1995; Lidicker 1999), few studies have addressed small mammal use of fire-induced edges, even though edges play an important role in the recovery of the fauna in burned areas (Larrivée et al., 2008; Santos et al., 2009; Tasker et al., 2011). For example, we know of only three studies on small mammal use of fire-induced edges (Figueiredo and Fernandez, 2004; Pires et al., 2005; Diffendorfer et al., 2012).

The habitat accommodation model (Fox 1982) has been proposed to explain small mammal succession in burned areas. This model relates small mammal re-colonization to post-fire changes in vegetation structure and composition, which also makes the model applicable to small mammal use of fire-caused edges. More recently, Ries and Sisk (2004) proposed a specific model to predict faunal distributions at edges of all types. Their model focuses on resource differences between the two juxtaposed habitats and the edge that separates them. In addition to creating sharp differences in vegetation, the edge separates habitats with markedly different food resources, risks of predation and abiotic factors. For example, in burned chaparral the early post-fire flora produces an abundance of seeds that may be missing, or occur at low densities, in unburned chaparral (Tyler and Borchert 2002). Moreover, as obligate seeding shrubs re-establish in the burn area, supplemental seeds may be abundant for several decades. On the other hand, unburned chaparral provides better protection from predators, especially in the early post-fire years. This asymmetry in resources creates conditions in which small mammals may increase their use of the edge because they can readily access an abundant food supply in the burn and at the same time find protection from aerial predators and carnivores in adjacent unburned chaparral.

In this study, we focused on small mammal use of a narrow zone (65 m) straddling burned and unburned chaparral on the main fire perimeter of a wildfire. Based on the Ries and Sisk model, we expected small mammals to increase their activity at the burn edge, especially in the early post-fire years when the seed supply increased in the burn area. However, as the edge softened in later years, and burned vegetation became increasingly similar to the unburned chaparral, we expected the attraction to the edge to be less pronounced, or to disappear altogether. Therefore, our objectives were (1) to describe small mammal use of a high-contrast edge over a 10-year period, and (2) to compare edge and burn-area use to existing studies of small mammal succession in burned chaparral at greater distances from the burn perimeter.

Methods

Study Area

In June 2002, the 8,100-ha Wolf Fire burned the two study sites situated on an extensive (~ 40 ha), old river terrace 30 m above Sespe Creek at 955 m elevation in Los

Padres National Forest. The study area is located 15 km NNE of Ojai, CA. The trapping grids were ~ 560 m NNW of the Sespe Trailhead (34° 33′ 38″ N, 119 ° 9′ 52″ W). Before the fire, the study area was dominated by 70-year-old chamise (*Adenostoma fasciculatum*) chaparral, with widely scattered dead chaparral whitethorn (*Ceanothus leucodermis*). Climate of the study area is Mediterranean consisting of cool wet winters and long dry summers. Average annual precipitation for Ojai, CA is 539 mm. From 2002–2010 precipitation was above average in five years and below average in four years.

The fire burned at unusually high intensity through the entire study area but was extinguished on the flat terrace ~ 120 m before reaching Sespe Creek. At the locations of the trapping grids, the boundary between burned and unburned chaparral was sharply defined because a 5-m wide bulldozer line was constructed as part of the fire suppression effort. On one side of the dozer line was a linear edge of unburned chaparral and on the burned side of the line a narrow (0.5 m–1.0 m) partially burned strip of vegetation left by the dozer we termed the "fringe". Beyond the narrow fringe was the expansive, denuded burn area. In the early years after the fire the cleared dozer line was sparsely vegetated but by nine years chamise cover was ~40%.

Small Mammal Trapping

We established two 8 × 12 trap grids 110 m apart. At each site, a row of 12 traps spaced 10 m apart was placed along the linear edge of the chaparral. Another row of traps was placed along the fringe five meters opposite the edge traps. Additional rows of traps were arrayed in the burn areas 15, 25 and 35 m perpendicular to the edge traps and 10, 20 and 30 m in the interior of the unburned chaparral. We used a single, large Sherman trap (10 cm × 12 cm × 38 cm) at each station.

We opened traps in the afternoon the first day and trapped for five days (four trap nights). Traps were baited with sunflower seeds and pieces of peanuts and walnuts. Cotton balls served as bedding. We checked traps each morning. Captured animals were marked at the base of the tail with a permanent marking pen, weighed, sexed, and assessed for reproductive condition. We used weight and pelage color to distinguish adult from sub-adult animals.

Trapping began in July 2002, one month after the fire. We trapped both grids in the spring (May–July) and fall (September–November) for the first five years post-fire (2002–2006). At the end of five years, several species lacked a sustained presence in the burned areas so we delayed trapping until the spring of 2008 and again in the spring of 2011 to monitor changes in their status in the burn areas.

Vegetation Methods

For each grid we estimated the cover of shrubs, herbs, forbs and grasses to the nearest 5% within 7-m^2 (radius 1.5 m) plots using the trap station as plot center. Cover was sampled at burn stations one, three and eight years post-fire and at the unburned stations one and eight years post-fire. To measure the vertical stratification of foliage at all the stations, we randomly chose 1 m^2 within each 7-m^2 macro-plot. We first estimated the total shrub cover and height in the 1-m^2 plot after which we placed a 2.5-m pole alternately banded in 50 cm increments at the plot center. The estimated cover of the 1-m^2 plot was partitioned among the 50-cm intervals marked on the pole.

Rodent Abundance

We used the Schnabel capture-recapture model to calculate the number of rodents per hectare in each trapping session. Densities are presented for the two grids combined

Table 1. Vegetation percent cover in burned chaparral in 2003, 2005 and 2010 and in unburned chaparral in 2003 and 2010. Values are means ± 1 SE.

	2003		2005	2010	
	Unburned	Burned	Burned	Unburned	Burned
Herbs, forbs, and grasses	0	31.4 ± 2.8	14.0 ± 2.7	0	0
A. fasciculatum	71.2 ± 1.8	19.7 ± 2.7	35.8 ± 3.4	69.5 ± 1.9	42.9 ± 2.2
C. leucodermis	0	0	2.0 ± 3.4	0	16.9 ± 2.1

which summed to 1.43 ha. Because animals were batch-marked, densities could not be calculated separately for burned and unburned areas.

Statistical Analysis

We spread fourteen trapping sessions over nine years. Sessions were lumped to create yearly intervals for analysis. For example, sessions at 1 and 6 months were combined for the early post fire period (year 0). Yearly intervals with their corresponding sessions are as follows: year one (11 and 14 months), year two (18, 22 and 24 months), year three (34 and 40 months), year four (46 and 51 months), year five (58 months), year seven (85 months) and year nine (107 months).

We used captures of each species to analyze the use of the four habitats over time: burned, fringe, edge and unburned. We analyzed habitat use by calculating the mean captures per trap (total captures in 4 nights) for 72 traps in the burned areas, 24 fringe traps, 24 edge traps and 72 traps in the unburned areas. Captures for the two grids were combined for the analyses since they were identical in rodent species composition and combining them increased the sample size. Because capture data were zero-inflated and failed to meet the assumptions of normality, we used Kruskal-Wallis analysis of variance to test for differences in captures per trap among the habitats for each of the eight years.

RESULTS

Vegetation Structure

The high-intensity fire completely denuded the burn area. All that remained immediately after the fire were exposed chamise burls with short (~15 cm), charred stems. Post-fire annual cover was highest in 2003 and was composed almost entirely of the annual short-lobed phacelia (*Phacelia brachyloba*) (Table 1). By 2005 the cover of annuals and short-lived perennials had all but disappeared in the burn.

Living chaparral whitethorn was absent in unburned chaparral but after the fire, seedling production by this shrub was prolific so that by 2005 cover had reached 2% (Table 1). Between 2005 and 2010 the cover and height of chaparral whitethorn increased rapidly and by 2010 it comprised 17% of the burn area shrub cover (Table 1). Chamise both resprouted and produced seedlings after the fire; its height and cover increased steadily in the burned area. After eight years, average total shrub cover did not differ significantly between burned and unburned stations (69.5% burned vs. 59.8% unburned, $t_{82} = -1.07$, P = 0.29) although shrubs still were taller in the unburned vs. the burned areas (178.5 cm unburned vs. 142.2 cm burned, $t_{81} = 6.02$, P $\leq$ 0.001).

The vertical foliage distribution was markedly different between burned and unburned vegetation eight years post-fire (Fig. 1). Compared to unburned chaparral, higher percentages of shrub foliage in the burned areas were in the 0–50 and 51–100 cm classes
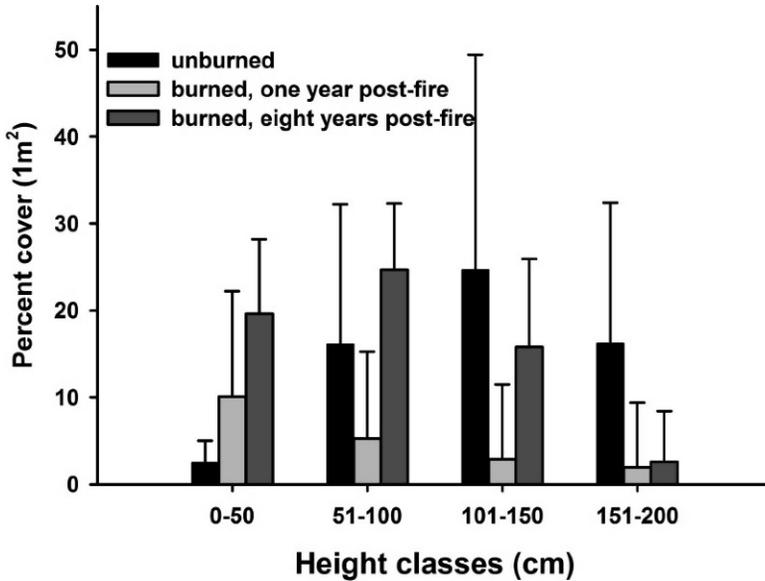
Fig. 1. Vertical stratification of shrub cover in 50-cm intervals for burned and unburned chaparral in the trapping grids. Unburned values are for one (2003) and eight years (2010) post-fire combined, and for burned chaparral one (2003) and eight (2010) years post-fire. Cover values are means ± 1 SE.

(Fig. 1). After nine years, the burn area remained more open with much of the foliage of the young shrubs concentrated in the lower strata. In unburned chaparral higher percentages of foliage were in the 101–150 and 151–200 cm classes but, unlike the burned stations, foliage was sparse in the near-ground stratum (0–50 cm) (Fig. 1). In the tallest layers of unburned chamise foliage and branches often formed a continuous, interlocking canopy.

Trapping Results

Between July 2002 and April 2011, 10,752 trap nights yielded a combined total of 778 captures of eight rodent species on the two grids. Based on the number of captures four species were relatively common and included: agile kangaroo rats (*Dipodomys agilis*) (224 captures), pinyon mice (*Peromyscus truei*) (218 captures), deer mice (*Peromyscus maniculatus*) (156 captures), and California mice (*Peromyscus californicus*) (170 captures). We also captured four Merriam's chipmunks (*Eutamias merriami*), four California ground squirrels (*Otospermophilus beecheyi*), one big-eared woodrat (*Neotoma macrotis*) and one brush mouse (*Peromyscus boylii*).

Agile Kangaroo Rats

Agile kangaroo rats initially were present in low numbers (Fig. 2a). At two years, density increased dramatically, primarily because juveniles made up half of the total. Density declined in the following years and remained relatively stable (Fig. 2a).

Captures were highest in the burn areas for three of the eight years (Fig. 3a). In the other five years captures were evenly distributed among the four habitats although burn-area captures slightly exceeded the other three habitats in each year (Fig. 3a). Kangaroo rats treated the fringe like the burned areas in the first three years. Captures in the burn areas peaked four and five years post-fire (Fig. 3a). Even though shrub cover increased
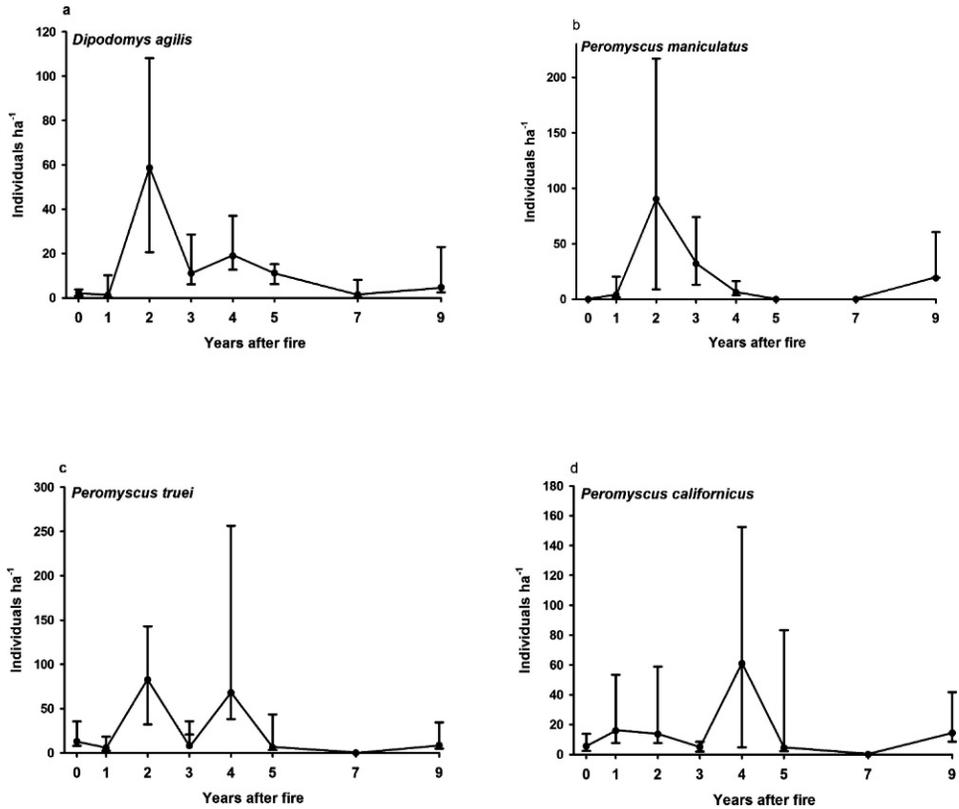
Fig. 2. a. *Dipodomys agilis* (agile kangaroo rat) density, b. *Peromyscus maniculatus* (deer mouse) density, c. *Peromyscus truei* (pinyon mouse) density, and d. *Peromyscus californicus* (California mouse) density. Values are for the total area of the grids: 1.43 ha. Error bars are the 95% confidence limits of the means.

and ground cover decreased after the fire, agile kangaroo rat captures remained relatively high in the burn areas until the conclusion of the study (Fig. 3a). Of the 50 sub-adult captures, 64% were in the burned areas, which was similar to adult captures (62%).

Deer Mice

Deer mice were not captured in three of the eight years making them the most variable of the three cricetids in terms of changes in density (Fig. 2b). Captures showed no significant difference among any of the habitats during the study (Fig. 3b). Adult and sub-adult males comprised 68% of the 68 captures in the burns.

Pinyon Mice

Pinyon mouse densities peaked in years two and four (Fig. 2c). Of the four species, pinyon mice consistently showed the highest mean captures in unburned chaparral in all eight years (Fig. 3c) and were least likely to enter the burn, although there was one short-lived increase in year two (Fig. 3c). Mean captures at the edge were highest in year 4 and were relatively high, but not statistically significant, in years zero, one, four, seven and nine (Fig. 3c). Of the 22 captures in the burns, 68% were adult and sub-adult males.
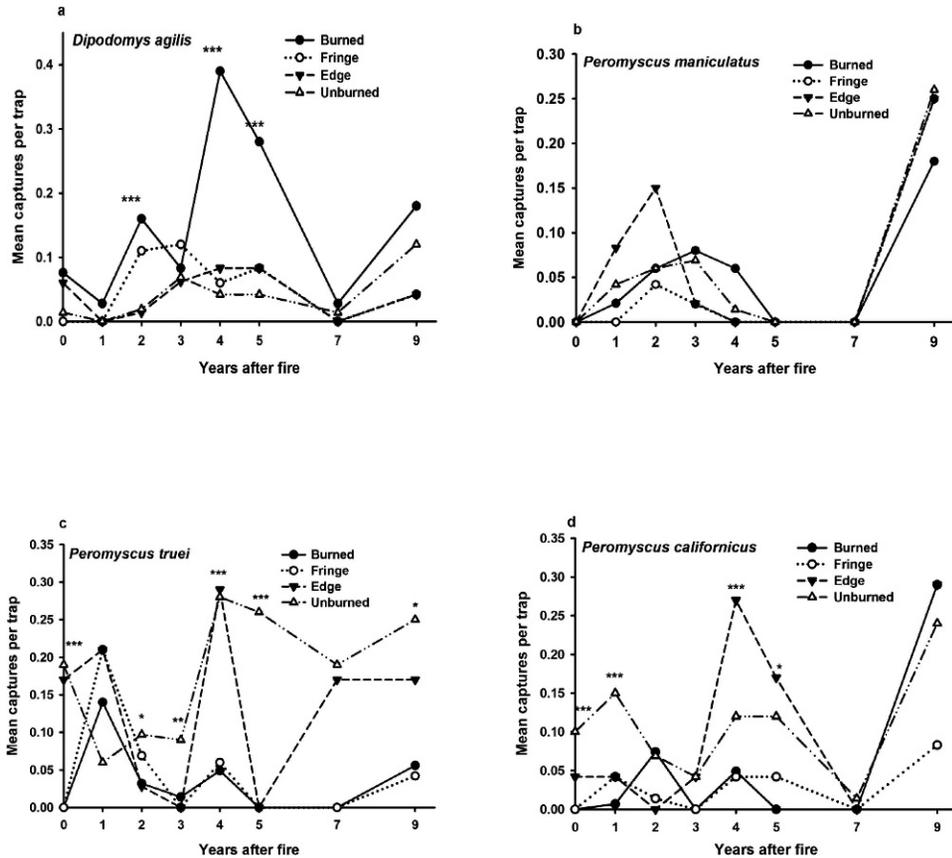
Fig. 3.   a. Mean captures per trap for *Dipodomys agilis* (agile kangaroo rat) in the burned areas (solid circle), fringe (open circle), edge (inverted solid triangle) and burned areas (open triangle), b. Mean captures per trap of *Peromyscus maniculatus* (deer mouse) for the four habitats, c. Mean captures per trap of *Peromyscus truei* (pinyon mouse) for the four habitats, and d. Mean captures per trap of *Peromyscus californicus* (California mouse) for the four habitats. Confidence intervals of the means have been removed for clarity. Asterisks indicate a significant difference in captures among the four habitats using Kriskal-Wallis ANOVA. Statistical significance is indicated as follows: * $p<0.05$, ** $p< 0.01$ and *** $p< 0.001$.

California Mice

The density of California mice was highest in year four (Fig. 2d). In the early years, California mouse captures were most prevalent in unburned chaparral but shifted to the edge in years four and five (Fig. 3d). Burn-area captures were highest in year nine. Of the 35 burn captures, 68% were adult males while just 2% were sub-adults.

Discussion

Based on what was known about the response of the four species to fire at the onset of this study, we expected them to enter the burns relatively quickly and, in fact, all appeared by 18 months post-fire, perhaps in response to seed production by post-fire herbs and forbs (Morris and MacEachern 2010; Plavsic 2011) . Agile kangaroo rats were captured most frequently in the burn areas (Fig. 3a). Deer mice, in contrast, were habitat generalists and were captured in all the habitats (Fig. 3b). Pinyon mouse captures were concentrated in in unburned chaparral throughout the study (Fig. 3c) although they

showed significant use of the edge in year four. California mouse captures were mostly confined to interior chaparral stations in the early years but shifted to edge and burned stations in years four and five (Fig. 3d).

In this study, kangaroo rats were strongly attracted to the open, burned areas. The prevalence of agile kangaroo rats in the burned areas was expected since it is a well-known early successional specialist (Wirtz 1977; Price et al., 1995; Quinn 1990; Schwilk and Keeley, 1998). Indeed, many *Dipodomys* spp. prefer open, newly burned habitats in a variety of vegetation types (Halford 1981; Brehme et al., 2011; Monasmith et al., 2010; Horn et al. 2011; Litt and Steidl, 2011).

Deer mice also readily occupied the burn area (Fig. 3b). This species is a habitat generalist and was edge-neutral. Deer mice are somewhat arboreal in chaparral (Laakkonen 2003) and are well-known for their ability to rapidly re-occupy burned areas (Quinn 1990; Price et al., 1995; Brehme et al., 2011). Indeed, deer mice are often the most abundant early burn rodents in an array of vegetation types (Larsen et al., 2007; Zwolak and Forsman, 2008; Fuhlendorf et al., 2010; Kirchner et al., 2011). In burned conifer forests, for example, deer mice populations increased soon after fire and became self-sustaining (Zwolak and Forsman, 2008). In fact, animals dispersed from burned into unburned habitats. In this study, deer mice trapped in unburned chaparral also may have come from populations in the burn area.

Based on Lawrence's findings (1966) for pinyon mice in northern California chaparral, we expected this species to enter the burn areas quickly in high numbers or perhaps to concentrate their activity at the edge where they had ready access seed produced by the post-fire annuals and short-lived perennials (Tasker et al., 2011). Instead, pinyon mice consistently were captured in unburned chaparral with only one notable increase (year one) in the burned areas (Fig. 3c). Edge use was significant in year four but also was relatively high in years zero, one, seven and nine (Fig 3c). Although frequently captured on the edge, pinyon mouse was not an edge specialist; it appeared to treat the edge as if it were unburned chaparral.

California mice are late-seral chaparral inhabitants (Merritt 1978; Quinn 1990) and have a negative response to fire (Lawrence 1966; Wirtz et. al., 1988; Brehme et al., 2011). We did not expect California mice to enter the burn early like pinyon mice, but we thought they might occupy the edge, or even the fringe, perhaps to take advantage of the early post-fire seed resource, and in later years, show an increase in the burn areas in response to increasing shrub cover, height and seed production.

Early in the study California mice captures were concentrated in unburned chaparral (Fig. 3d). However, by years 4 and 5 California mouse captures increased markedly at the edge, although they also continued to be relatively high in unburned chaparral (Fig. 3d). In those two years this species may have been an edge specialist. If so, it is not clear why since *Ceanothus leucodermis*, which began to produce seeds in the burned areas in year four, was absent in the space between the edge and fringe. Finally, burn-area occupation by California mice was intermittent (years two, four and nine), supporting other studies that have reported the irregular appearance of California mice in the early post-fire years (Quinn 1990), especially after high severity fires (Wirtz 1995). California mice in burned chaparral were more abundant near unburned vegetation than at sites farther from refugia (Schwilk and Keeley, 1998; Diffendorfer et al., 2012).

Small mammal re-occupation of burns is often closely linked to structural vegetation recovery (Fox et al., 2003; Di Stefano et al., 2010) as well as seed production (Suazo et al.,

2013). According to the habitat accommodation model (Fox 1982), small mammals sequentially re-enter disturbed habitats when their species-specific vegetation require-ments are met, *e.g.*, when its optimum height or cover values are attained. As the optimum vegetation requirements of a species develop, its abundance increases, but then declines as the vegetation moves away from its optimum (Monamy and Fox, 2000; Fox et al., 2003). In this study, agile kangaroo rats increased in the open burn areas (its optimum) but are expected to decrease as the cover and complexity of late-seral chaparral returns (Quinn 1990).

In contrast, the habitat distributions of California mice and pinyon mice suggest the vegetation structure in the burn has yet to reach their re-occupation optima. Both species are highly arboreal in late-seral shrublands (Meserve 1972; Laakkonen 2003). Although we did not trap the shrub canopies, it is possible that a more permanent presence of these species in the burned areas depends on the development of a more complex shrub canopy, *i.e.,* one more conducive to arboreal activity. The tall canopy layers and intermingled branches characteristic of late-seral chamise chaparral have yet to fully develop in the burns after ten years (Fig. 1).

Studies of post-fire succession of small mammals in chaparral have been relatively short in duration, lasting one to seven years (Wirtz 1995; Schwilk and Keeley, 1998) and have focused primarily on the first arrival of species in burn areas. For some species, however, the early post-fire years may be only the beginning stage of a much longer period of re-occupation. In a chronosequence study of small mammal succession in Australian tree mallee, Kelly et al. (2011) showed that colonization of recovering burns occurred rapidly for some species but required many decades for others. For example, house mice (*Mus domesticus*) quickly re-occupied (< five years) burns dominated by bare ground. However, this initial surge in abundance was followed by a decline until it was rare in burns older than 20 years. In contrast, the late successional southern ningaui (*Ningaui yvonneae*) was missing from recent (<14 months) burns. Instead, males attained their maximum abundance at ~25 years post-fire and females did not peak until ~30 years. Most notably, breeding females did not reach a maximum until ~45 years. In this study, agile kangaroo rats and deer mice quickly occupied the burns and appeared to have a sustained presence there over the ten years. In contrast, pinyon mice and California mice mainly inhabited unburned chaparral and only intermittently entered the burns. Throughout the study, males dominated burn captures of the latter two species suggesting they were still in the early phases of re-occupation (Southerland and Dickman, 1999).

Because we studied a small portion of the burn perimeter, our results have limited application to the rest of the burn. Nevertheless, one of our main conclusions is that previous studies of chaparral small mammal succession may have described only the earliest phases of post-fire re-occupation by late-seral small mammals and that there is a need to address longer time periods perhaps using a chronosequence approach. After a decade, pinyon mice and California mice have yet to regularly occupy the burns and most early colonists of these species were males. Clearly, studies lasting < 10 years may not be long enough to describe the complete re-entry of these species. Trapping chaparral burns of different ages offers the opportunity to gather both demographic and habitat requirement data over a longer time period. Using this approach, it would be possible to examine how the proportion of males and females occupying recovering chaparral changes over time, as well as to determine when reproductive females become permanent members of the small mammal community.

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