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Wildfire and rodents

Effects of large-scale wildfires on rodents in southern California

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In October 2003, wildfires burned large areas of San Diego County. After the wildfires, we surveyed rodents in both burned and unburned plots across four sites and four vegetation types (coastal sage scrub, chaparral, woodland and grassland) using a combination of pitfall and Sherman live-traps and prefire data at one of the sites. We analyzed the effects of fire on the community structure and relative abundance of rodents across these vegetation types. Multivariate analyses revealed that all postfire rodent communities more closely resembled each other than they did prior to the burn. There were significant postfire differences in rodent community composition for coastal sage scrub, chaparral and grassland. Individual rodent species largely responded in a manner consistent with their life history characteristics. Generalist and open habitat specialists typically increased in relative abundance, while closed habitat specialists decreased. Among vegetation types, there were significant increases in relative abundance of the deer mouse (*Peromyscus maniculatus*) and Dulzura kangaroo rat (*Dipodomys simulans*). In contrast, significant decreases in relative abundance were found for the California mouse (*Peromyscus californicus*), San Diego pocket mouse (*Chaetodipus fallax*), desert woodrat (*Neotoma lepida*) and the brush mouse (*Peromyscus boylii*). We discuss our results in relation to the management and conservation planning of these natural areas under a scenario of larger and more frequent wildfires in southern California.

Key words**:** *Chaetodipus*, chaparral, coastal sage scrub, *Dipodomys,* fire, grassland, *Neotoma, Peromyscus,* small mammals, woodland.

Wildfires have long been a part of the natural and human altered environments of southern California. Despite fire suppression efforts and management plans, large and small wildfires continue to occur from both natural ignition sources and increasingly from those associated with increasing human population (Keeley et al 2004). As a result, the intervals between fires have been substantially reduced when compared to historic levels, resulting in an overall increase in fire frequency. Although native vegetation communities of southern California have evolved various survival strategies to adapt to the natural fire regime (Hanes 1971; Keeley and Fotheringham 2001; Keeley and Keeley 1981, 1984; Vogl and Schorr 1972; Zedler et al. 1983), repeated fires can cause type conversion of chaparral and coastal sage scrub shrublands into grasslands (Keeley 2005; Zedler et al. 1983). This change in fire regime will likely have short and long term impacts on native wildlife communities which include many rare and endemic species (Diffendorfer et al. 2007).

Fire can have both direct and indirect effects on animal communities. Individuals may suffer immediate mortality as a result of suffocation or direct exposure to lethal levels of heat (Howard et al. 1959; Lawrence 1966). Fire can contribute indirectly to rodent mortality by altering the surrounding vegetation, resulting in the loss of suitable habitat and food resources (Chang 1996; Price et al. 1995). Alternately, the postfire environment may contain open or disturbed habitat allowing for improved movement, foraging, and reproductive opportunities for some rodent species (Price et al. 1995).

In October of 2003, fires consumed approximately 300,000 hectares (ha) in southern California. This included approximately 130,000 ha in San Diego County from both the Cedar and Otay fires. In addition to the loss of nearly 5,000 structures and 15 human fatalities (CDF 2003), these large fires likely affected local wildlife communities in a region already recognized as being one of the most at risk areas for loss of biodiversity (Mittermeier et al. 1997). The first large habitat reserve created in San Diego County, the Multiple Species Conservation Plan (MSCP; City of San Diego 1997) lies directly in the footprints of these two fires. Half of the protected lands within the MSCP were affected by the fires and some protected habitats were entirely burned. In order to make informed management and future reserve design decisions, it is important to identify the species most at risk for population declines or extirpations due to fire. Knowledge of species responses to fire in relation to their life history traits and habitat preferences should aid in identifying those most at risk and in predicting the effects of fire on unstudied species and habitats.

Rodents have many functional roles in the environment. As a food source for many predators, they serve as important links between producers and higher level consumers. Rodent burrows provide shelter for many species, serve to aerate the soil, and aid in the sinking of surface water. Rodent communities are important components of vertebrate biomass and biodiversity (Converse et al. 2006) and by consuming and distributing seeds, they affect successional patterns and vegetation characteristics in many habitats (Brock and Kelt 2004; Price and Jenkins 1986; Tevis 1956).

Our study took place in four locations within San Diego County, one high elevation and three low elevation sites. The objectives of this study were to determine 1) the effects of fire on rodent community composition for four vegetation types in southern California (coastal sage scrub, chaparral, grassland, and woodlands) and 2) if individual species responses were consistent with their habitat preferences and life history characteristics.

MATERIALS AND METHODS

Study Sites.–The study areas were located on four properties: Rancho Jamul Ecological Reserve-Hollenbeck Canyon Wildlife Area (Rancho Jamul), Otay Mountain Wilderness-Little Cedar Ridge (Little Cedar), Santa Ysabel Open Space Preserve (Santa Ysabel) and Elliott Chaparral Reserve (Elliott). All sites were in San Diego County, California (Fig. 1).

Rancho Jamul Ecological Reserve and adjacent Hollenbeck Canyon Wildlife Area are located in the lower foothills of southwestern San Diego County (California, United States) approximately 30 km from the coast. Rancho Jamul is dominated by coastal sage scrub, oak and sycamore woodlands, native and non-native grasslands and riparian vegetation. Dominant plant species at the site include brome grass (*Bromus spp.*), wild oats (*Avena spp.*), California buckwheat (*Eriogonum fasciculatum*), California sage (*Artemisia californica*), coast live oak (*Quercus agrifolia*), western sycamore (*Platanus racemosa*), laurel sumac (*Malosma laurina*), and San Diego sunflower (*Viguiera laciniata*). The property is 2,797 ha in size (including adjacent Hollenbeck Canyon Wildlife Area) with an average elevation of 250 m. The Otay Fire burned the southern portion of this site in October 2003.

Little Cedar is located 6 km south of Rancho Jamul on the northern slopes of Otay Mountain. It is dominated by coastal sage scrub, mixed chaparral and cypress forest. The dominate plant species at the site are chamise (*Adenostoma fasciculatum*), Tecate cypress (*Cupressus forbesii*), annual non-native grasses (*Avena* and *Bromus*), and

California buckwheat (*E. fasciculatum*). The property is 6,800 ha in size and ranges from 250 to 1,000 m in elevation and was completely burned in the Otay Fire of 2003.

Santa Ysabel spans the upper foothills and lower mountains of north-central San Diego County approximately 60 km from the coast and is dominated by oak and pine woodlands, native and non-native grasslands, costal sage scrub, chaparral, and riparian vegetation. Plant species dominating the various habitats are coast live oak (*Q. agrifolia*), brome grass (*Bromus*), chamise (*A. fasciculatum*), Engelmann oak (*Quercus engelmannii*), wild oats (*Avena*), and white sage (*Salvia apiana*). This property is 2,188 ha in size (including both East and West properties) with an average elevation of 1,078 m. In 2003, half of the East property was burned in the Cedar Fire.

Elliott is located approximately 25 km from the coast. It is predominately coastal sage scrub and chaparral, with chamise (*A. fasciculatum*), California buckwheat (*E. fasciculatum*), and annual non-native grasses (*Avena* and *Bromus*). The property, while only covering 43 ha within its boundaries, is bordered by expansive open space in the Marine Corps Air Station Miramar and has an average elevation of 195 m. The entire property was burned in October 2003 by the Cedar Fire.

More detailed information on fire severity and distance to unburned refugia for our study sites are presented in Rochester et al. (In Press).

Plot selection.–Plot locations were selected within one of four vegetation types: chaparral, coastal sage scrub, grassland and woodland.

In the summer and fall of 2001 and 2003, we surveyed rodents at one of our sites, Rancho Jamul, at 16 study plots in coastal sage scrub and grassland. In 2005 and 2006, two and three years following the 2003 wildfires, we surveyed for rodents in burned and unburned habitats at 63 study plots across all four sites using the same methods. Each site was sampled four times per year, twice in the spring and twice in the fall. Table 1 shows the number of plots surveyed by vegetation type and site both before and after the fires.

Trap Arrays.–All study plots consisted of an array of pitfall traps, funnel traps, and Sherman live-traps. The pitfall trap array contained seven 19 liter buckets. Each bucket was buried flush with the ground and connected by shade cloth drift-fence forming a “Y” shape. Each of the three arms was approximately 15 m long. One funnel trap was placed along each arm between the two outer buckets. Nine pairs of Sherman live-traps were distributed around the pitfall array, each pair composed of one small trap (8 x 9 x 30.5 cm) and one large trap (10 x 11.5 x 38 cm). All traps within a plot were opened for four consecutive days and closed at the end of the fourth day. Pitfall and funnel traps were left unbaited as passive traps for mammals. Sherman traps were baited with steam-rolled oats and insulated with polyester batting. All traps were set in the late morning or early afternoon and checked each day beginning at sunrise. Traps were closed securely or removed to prevent incidental captures or mortality between sample sessions.

All animals were handled and processed in a humane manner as approved by USGS Animal Care and Use Committee and in accordance with ASM guidelines (ACUC 1998). Rodents were identified to species, weighed, measured (head and body, tail, hind foot, and ear length), and assessed for gender, reproductive condition, and age class. To identify animals recaptured within a sample session, all animals were temporarily marked by hair clipping.

Vegetation Surveys. –Vegetation surveys were conducted once at each plot before the 2003 wildfires and again in the spring of 2005 and 2006 (Fisher et al. 2002; Laakkonen et al. 2001). At 0.5 m intervals along a 50 m linear transect, we recorded plant species, canopy height, leaf litter depth, and substrate type, for a total of 100 data points per plot (Sawyer and Keeler-Wolf 1995). The results of the prefire vegetation surveys were used to classify each plot into one of the four vegetation types (coastal sage scrub, grassland, woodland, and chaparral).

Data Classification and Reduction. –A before-after reference-impact approach (BARI) was used to classify the data for univariate tests (Smith 2002; Stewart-Oaten et al. 1986; Underwood 1994). In this process, we classified each sample as either a reference or an impact plot. All plots burned during the 2003 wildfires were classified as impact plots while all plots unburned during the wildfires were reference plots. Reference and impact classification also applied to both the prefire time period when all plots existed in an unburned condition and the postfire time period when impact plots burned either wholly or partially (Table 1). We used this BARI classification for assessing and describing the effects of the fires on vegetation cover and rodent species abundance.

For the multivariate analyses, the fire classification was condensed into two categories: razed and nonrazed. This allowed us the power to test whether fire had a significant effect on community structure within each vegetation type. In terms of the BARI classifications described above, nonrazed refers to all data collected in the prefire surveys (before reference and before impact) plus the postfire surveys at unburned plots (after reference). Razed refers to all data collected in the impact plots (after impact) after the 2003 wildfires. Table 1 identifies the terms used in the analysis of the rodent species.

We carefully reviewed these data individually on MDS plots to ensure that the pooling of unburned reference and impact plots was valid (i.e. did not group out as separate clusters).

Statistical Analysis.–The capture rates of rodents are highly variable over short time periods due to their activity levels in relation to daily and seasonal environmental factors. To reduce seasonal and daily variability, we averaged the number of captures for each species across sample sessions for the time periods both before and after the wildfire. The averaged prefire and postfire capture rates with sample plots treated as replicates were used as the basis for all further analyses.

In order to explore large scale patterns in the data, capture rates were averaged by vegetation type and fire condition (razed and nonrazed) and a Bray-Curtis similarity matrix of the data was created. The similarity among sample plots and fire condition were then plotted using nonmetric multidimensional scaling (MDS). In an MDS plot, samples which are relatively close together can be interpreted as more similar, while those that are more distant are interpreted as more dissimilar. We used hierarchical agglomerative cluster analysis with group-average linking to examine the degree of similarity between razed rodent communities in comparison to the nonrazed communities. We then overlaid species abundance vectors on the MDS plot to visualize the directional response of species abundance in relation to razed and nonrazed vegetation types (Clarke and Warwick 2001; Clark and Gorley 2006).

To determine if fire significantly affected rodent community structure within vegetation types, we first tested whether the factors of vegetation type, site, or both were significantly predictive of community structure using two-way crossed analysis of similarity (ANOSIM) tests of square root transformed data. ANOSIM is a multivariate permutation-based test which is similar to the two-way analysis of variance test in univariate statistics (Clarke 1993). If vegetation type was significant, the effect of the fire was tested separately for each. If site was significant, it was controlled for by inclusion as a fixed effect in subsequent individual ANOSIM tests. We also used the biological – environmental matching (BIOENV) statistical routine to determine if the total cover of shrubs and trees was significantly associated with these biotic patterns. We then analyzed the changes among individual species in the community using univariate methods described below.

We tested for effects of the fire on the relative abundance of individual species within vegetation types in two ways. First, using postfire data from all of our sites and plots, we generated general linear mixed-models of capture rates with site as a random factor, and species and burn status as fixed factors. This was done separately for each vegetation type. Contrast tests were conducted to test whether relative abundance of species at the impact plots differed from that of the reference plots. Variances were pooled across species and sample plots within each vegetation type. Second, for the impact and reference plots that we had both prefire and postfire data (Rancho Jamul: coastal sage scrub and grassland), we subtracted the prefire capture rate from the postfire capture rate for each species at each plot to produce a ‘net change after fire’ statistic. We then ran a two-way ANOVA with species and burn status (reference vs. impact) as fixed factors. The differences of least squares means were used to test whether the change in abundance at the impact plots were significantly different from the change in abundance at the reference plots. Probability values ≤ 0.10 were used to assess statistical significance across all tests. Multivariate analyses were performed with Primer-E software (Primer E Ltd. 2006) and univariate analyses were performed with SAS software (SAS Institute Inc 2002-2003).

RESULTS

Vegetation structure.– We found significant differences in shrub and tree cover in two of the four habitats, coastal sage scrub and chaparral (Table 2). Coastal sage scrub and chaparral fire impacted plots had 77% and 53% reductions in shrub and tree cover compared to reference plots, respectively. Reductions in grassland and woodland shrub and tree cover were not significant, ranging between 33 and 35% loss respectively. Coastal sage scrub impact plots also had an average of 30% more cover from forbs. Forb cover did not significantly differ between reference and impact plots for the other vegetation types. Grass cover did not differ between reference and impact plots in any vegetation type (Table 2).

Overall Trapping Results.–We captured 16 small mammal species across all vegetation types for a total of 4,444 captures prefire and postfire. The most common captures included the deer mouse (*Peromyscus maniculatus*), Dulzura kangaroo rat (*Dipodomys simulans*), San Diego pocket mouse (*Chaetodipus fallax*) and the harvest mouse (*Reithrodontomys megalotis*). Other species captured were the California pocket mouse (*Chaetodipus californicus*), California vole (*Microtus californicus*), desert woodrat (*Neotoma lepida*), dusky footed woodrat (*Neotoma macrotis*), brush mouse (*Peromyscus boylii*), California mouse (*Peromyscus californicus*) and the cactus mouse (*Peromyscus eremicus*). We also documented the presence of Botta's pocket gopher (*Thomomys bottae*), desert shrew (*Notiosorex crawfordi*), ornate shrew (*Sorex ornatus*), house mouse (*Mus musculus*) and the California ground squirrel (*Spermophilus beecheyi*). These last five species were captured only rarely so were not used in any of the analysis.

Postfire Multivariate Community Analyses.–Multi-dimensional scaling graphs and hierarchical clustering showed that across vegetation types, the rodent communities from razed plots more closely resembled each other than the corresponding nonrazed rodent communities (Fig 3A). Using group-average linking, razed coastal sage scrub, chaparral, grassland and woodland merged into a single group at a similarity level of 59.2%. This is in contrast to the nonrazed communities that only merge at a similarity level of 38.2% (Fig 3B). Vectors of individual species abundance in relation to the razed and nonrazed rodent communities showed positive responses for both *P. maniculatus*, and *D. simulans* to the razed communities, while *P. californicus, P. boylii, C. fallax, C. californicus, Microtus californicus, N. lepida, P. eremicus* vectors showed positive responses to nonrazed communities. The *R. megalotis* response was less clear, with increased abundance along a vector lying between both nonrazed and razed woodlands and razed grasslands (Fig 2C).

ANOSIM tests showed significant differences in composition of the rodent communities among vegetation types and sites ($R_{veg} = 0.35$, $n = 63$, $P = <0.001$, and $R_{site} = 0.27$, $n = 63$, $P <0.001$). Therefore, analyses of the burn effects were conducted for each vegetation type separately, controlling for site as a fixed effect. These analyses showed that rodent community composition in razed plots was significantly different from the composition in nonrazed plots in coastal sage scrub ($R = 0.23$, $n = 29$, $P = 0.050$), chaparral ($R = 0.714$, $n = 16$, $P = 0.067$) and grassland ($R = 0.40$, $n = 19$, $P =$

0.021) but not woodland ($R = 0.009$, $n = 18$, $P = 0.444$). Results of the BIOENV further showed that the percentage of shrub and tree cover was associated with rodent community composition for coastal sage scrub ($\rho = 0.195$, $n = 29$, $P = 0.005$; Fig. 4) and woodland ($\rho = 0.216$, $n = 18$, $P = 0.104$), but not chaparral ($\rho = 0.053$, $n = 16$, $P = 0.294$) or grassland ($\rho = 0.021$, $n = 19$, $P = 0.554$).

Differences in single species relative abundance.–The relative abundance and differences in relative abundance of rodent species at postfire reference and impact plots within each vegetation type are presented in Figs. 4-7. For coastal sage scrub and grassland vegetation in Rancho Jamul, where we had both prefire and postfire data, results of contrast tests are presented in Fig. 8.

In coastal sage scrub reference plots, the relative abundance of 11 rodent species were evenly distributed (i.e., all within a factor of four). In the impact plots, however, *P. maniculatus* and *D. simulans* were highly abundant dominants in the community (Fig. 4A). The difference in the relative abundance was significant for four species. *P. maniculatus* (Diff = 2.53, $se = 0.92$, $t_{209} = 7.49$, $P = 0.006$) and *D. simulans* (Diff = 1.69, $t_{209} = 3.33$, $se = 0.92$, $P = 0.069$) were more abundant in impact plots. Conversely, *P. californicus* (Diff = -1.61, $se = 0.92$, $t_{209} = 3.00$, $P = 0.084$) and *N. lepida* (Diff = -2.01, $se = 0.92$, $t_{209} = 4.74$, $P = 0.031$; Fig. 4B) were less abundant. All other species were less abundant on average, but not significantly, on plots impacted by the fires. Paired contrasts tests between the four impact and four reference plots in coastal sage scrub at Rancho Jamul also showed a significant increase in *D. simulans* abundance (Diff = 3.34, $se = 1.914$, $t_{41} = 1.75$, $P = 0.088$), but not *P. maniculatus* (Diff = -0.69, $se = 1.56$, $t_{41} = 0.44$, $P = 0.662$), as this species also increased at the reference plots after the fire (Fig

8A). In comparison to the larger postfire results, there was also an insignificant decrease in *N. lepida* (Diff = -1.02, *se* = 1.69, t_{41} = 0.60, *P* = 0.548). *P. californicus* was not captured at these plots.

In grassland reference plots, *C. fallax* and *P. maniculatus* were the top two dominant species (Fig. 5). The relative abundance of *C. fallax* was significantly lower in grassland impact plots (Diff = -1.83, *se* = 0.57, t_{99} = 10.45, *P* = 0.002), leaving *P. maniculatus* dominant. *C. fallax* abundance also significantly decreased at the four impact and four grassland reference plots at Rancho Jamul (*C. fallax* Diff = -5.44, *se* = 0.98, t_{19} = 5.54, *P* < 0.001; Fig 8B).

In chaparral reference plots, *P. californicus* and *P. eremicus* were the top two dominant species (Fig. 6A), while *P. maniculatus* and *D. simulans* were both highly abundant and dominant in the fire impacted plots. Results in chaparral were very similar to coastal sage scrub, as *P. maniculatus* (Diff = 5.35, *se* = 1.23, t_{154} = 19.04, *P* = <0.001) and *D. simulans* (Diff = 2.76, *se* = 1.23, t_{154} = 5.10, *P* = 0.025) were substantially and significantly more abundant on impact plots, while *P. californicus* (Diff = -2.24, *se* = 1.228, t_{154} = 3.32, *P* = 0.07) was significantly less abundant. All other species were less abundant on average on impact plots, but not significantly (Fig. 6B).

In the woodland reference plots, *P. maniculatus* and *P. boylii* were codominants. In the fire impacted plots, however, the relative abundance of *P. maniculatus* was double its abundance on the reference plots (Diff = 2.42, *se* = 0.63, t_{143} = 14.50, *P* = 0.002), and *P. boylii* abundance was 90% lower than the reference plots, making it a minor component of the postfire community (Diff = -1.77, *se* = 0.63, t_{143} = 7.68, *P* = 0.006).

Other species showed very little differences in abundance across reference and impact plots (Fig. 7A-B).

DISCUSSION

Rodent Community Response to Fire.–The results of our study indicate the coastal southern California rodent community exhibits a strong response to wildfire within the first two to three years after the fire. Overall, the rodent communities of the burned habitats were much more similar to each other after the fire. This response was consistent across vegetation types in that the generalist deer mouse, *P. maniculatus*, became the dominant member of all four vegetation communities studied, coastal sage scrub, chaparral, grasslands, and woodlands. Other rodents also largely responded in a manner consistent with their microhabitat and food preferences. For instance, the open habitat seed specialist, *D. simulans*, increased in multiple habitats, while the closed habitat shrub specialists, *P. californicus, N. lepida, and P. boylii* decreased.

Habitat for closed shrub specialists was substantially and significantly reduced in the razed coastal sage scrub and chaparral communities, with losses of 77% and 53% shrub and tree cover, respectively. The wildfires had less severe effects on woodland shrubs and trees with the loss in cover averaging 35%. The loss in vegetation structure undoubtedly affected the relative abundances of rodent species. This was supported by the significant correlation of rodent composition with the percent cover of shrubs and trees in coastal sage scrub and woodlands. We expect rodent composition was also correlated with shrub and tree cover in chaparral, however, we lacked the statistical power due to having few nonrazed plots.

Multivariate tests for the effects of fire on rodent communities showed significant differences in rodent community composition in razed versus nonrazed coastal sage scrub, grassland and chaparral. These riparian environments contain high levels of moisture, likely allowing them to maintain much of their prefire structure and act as refugia for the animals sheltering within (Chang 1996). Although the rodent community in razed grasslands was significantly different than nonrazed plots, grasslands experienced no significant change in vegetation structure as measured by shrub, grass, or forb cover.

Individual Species Responses.–The postfire changes in these rodent communities were likely caused by both direct and indirect effects of the fires. Direct effects include differences in species mortality, while indirect effects may include changes in habitat suitability as well as competitive and predator-prey interactions.

Some studies suggest little evidence of direct mortality among rodents from fire (Howard et al. 1959; Lawrence 1966). During fires, many rodents are able to escape by seeking refuge in burrows and rocky outcrops (Chang 1996; Howard et al. 1959; Shaffer and Laudenslayer 2006; Whelan 1995) where they are protected due to the insulating properties of soil (Quinn 1979). Lawrence (1966) suggests that the likelihood of survival is greater if a burrow has multiple openings for ventilation and maintains a vapor pressure under 40 mmHG. Those species living above ground in flammable shelters run a higher risk of mortality (Whelan 1995). The degree of impact may also be associated with the timing of nesting, mating, breeding, foraging, and periods of inactivity (Shaffer and Laudenslayer 2006). A fire occurring during the time of year when young are restricted to the nest would have higher consequences for any offspring unable to move quickly or too young to fend for themselves.

Indirectly, fire alters and opens up the habitat, changing its suitability for many species (Cook 1959; Keeley 2001; Lawrence 1966). Survivors that depend or prefer closed habitat may move to another location in search of suitable shelter and food. Within coastal sage scrub, chaparral, and woodland, we observed a decrease in relative abundance for rodent species associated with closed habitats or trees and shrubs (*N. lepida, P. californicus, P. boylii*), as well as an increase in generalist species and those associated with open habitats and bare ground (*P. maniculatus, D. simulans*—Cook 1959; Lawrence 1966; Price et al. 1995; Schwilk and Keeley 1998; Wirtz et al. 1988; Table 3).

N. lepida significantly decreased in coastal sage scrub. *Neotoma* species build large nests above ground in rocks, trees and vegetation using woody materials and debris. *N. lepida* is abundant in rocky outcrops and cliffs and on slopes with dense canopies (Price and Waser 1984; Verts and Carraway 2002). The decrease in the relative abundance in burned coastal sage scrub was likely due to mortality from the combustion of their above ground nests as the fires occurred. However, some *N. lepida* living in rocky outcrops with sufficient retreats may have survived. The populations may be depressed into the near future due to lack of suitable materials with which to build new nests (Wirtz et al.1988). We did not have enough data to evaluate the response of the other species of woodrat, *N. macrotis*, as it was present in only a few of our sites. Because of its similar life history, we would expect it to experience similar declines.

We observed significant decreases in the relative abundance of *P. californicus* within burned chaparral and coastal sage scrub communities. This species has strong food preferences for shrub fruits, seeds, and flowers (Meserve 1976a, 1976b). For habitat, this species prefers chaparral and dense coastal sage scrub (M'Closkey 1972) and shelters in burrows and woodrat nests (Grinnell and Orr 1934; Merritt 1974). Mortality from fire and reduced habitat suitability from the thinning of burned chaparral and coastal sage scrub habitats are likely reasons for the significant decreases observed for this species. This is consistent with other studies such as Lawrence (1966) who found that *P. californicus* was unable to maintain prefire numbers in the altered postfire environment. Wirtz et al. (1988) found that the postfire populations of *P. californicus* never reached prefire numbers in the more severely burned areas even after four years.

There was a significant decrease in relative abundance for *P. boylii* in woodland plots. *P. boylii,* like *P. californicus*, is a shrub and tree specialist. *P. boylii* are arboreal, commonly using trees, logs and shrub canopies for foraging and nesting (Holbrook 1979, Kalcounis-Rüppell and Millar 2002, Jameson and Peeters 2004). Their diet is largely composed of acorns (*Quercus sp.),* Manzanita berries, and fruits and seeds from a variety of shrubs and trees (Baker 1968, Jameson and Peeters 2004). Their decreases after the fire are expected as *P. boylii* are consistently found in higher abundances in areas with medium to high densities of shrub and tree cover (Holbrook 1979, Quinn 1990, Roberts et al. 2008).

Chaetodipus fallax numbers showed a significant decrease in burned grassland. This species is a granivore with a diet consisting of large amounts of seeds from both annual forbs and grasses (Meserve 1976a). The preferred habitats of *C. fallax* tend to be sparsely vegetated areas with sandy soils suitable for digging burrows (Lackey 1996; Price and Waser 1984). Since this species is typically associated with open habitats, we expected an increase in numbers due to an increase in suitable habitat. It is unknown to what degree direct mortality may have contributed this decrease. *C. fallax* are known to use the surrounding plants and rocks as cover from predators while searching for food (Lackey 1996). It is possible that the clearing of plant cover by the fire may have had a negative effect on this species by increasing their vulnerability as prey. Price et al. (1995) also noticed that *C. fallax* was more abundant in their unburned plots.

In burned coastal sage scrub and grasslands, there were insignificant, but marked decreases in the relative abundance of *M. californicus.* This species is dependent on systems of burrows and runways in grasslands for movement and foraging (Stark 1963). In compact clay soils, typical in southern California grasslands, *M. californicus* largely prefer to forage and nest above ground (Stark 1963). This species also has small home ranges and displays high site fidelity, even in the face of imminent danger. In fact, they have been known to stay and drown within their home ranges during flooding events, rather than seek shelter upland (Stark 1963). These life history traits may contribute to significant direct mortality of *M. californicus* during fire events in grasslands. Work by Cook (1959) and Pearson (1959) indicates that *M. californicus* require at least one year worth of growth before the vegetation provides the desired level of cover. Since our study took place in the second and third years after the fire, when grasses were abundant, we hypothesize that this species was likely impacted by direct mortality from the fires.

Some rodent species were able to take advantage of the conditions resulting from fire. *P. maniculatus* was the most abundant species in fire impacted plots across all habitats. This is in comparison to the reference plots, where *P. maniculatus* was not dominant. This species is a habitat and dietary generalist that is abundant in a wide variety of disturbed and undisturbed habitats eating a variety of plants, seeds and insects (Cook 1959; Jameson 1952, Holbrook 1978; M'Closkey 1972). *P. maniculatus* has been documented to be a frequent invader after fire (Converse et al. 2006; Holbrook 1978; Lawrence 1966; Meserve 1976b; Schwilk and Keeley 1998) where it is likely attracted by the abundant seed bank and new growth, as well as by the decreased competition from other rodents. Cook (1959) found that *P. maniculatus* remained at a constant or higher density in burned plots compared to unburned. *P. maniculatus* is also able to reproduce quickly having multiple gestations within a year allowing for a rapid increase in abundance. At our Rancho Jamul site, where we monitored four coastal sage scrub reference and impact plots before and after the fire, we found increases in *P. maniculatus* postfire abundance in both reference and fire impacted plots. Since this study site was patchily burned, we believe this may have been due to a spillover effect, where high densities of *P. maniculatus* in burned areas invaded nearby unburned areas.

We found a significant increase in the relative abundance of *D. simulans* in burned coastal sage scrub and chaparral. This species prefers open habitat associated with coastal sage scrub and chaparral (Kelt et al. 2005). *D. simulans* is a bipedal heteromyid rodent that prefers bare ground on gentle slopes. *D. simulans* is opportunistic in the collection of seeds which, according to Kaufman et al. (1988) become easier to find after fire. Wright and Bailey (1982) suggest that many seeds are not destroyed by fire and remain a viable food source. With the removal of dense vegetation during the fires, *D. simulans* invaded the newly open habitat where it could take advantage of the resulting foraging opportunities.

Overall, individual species results were consistent with those found in other studies (Table 3) and help to contribute to our knowledge of species responses across a wider array of habitat types in southern California. In this study, we did not have the power to assess the impact of the fires on some of the less abundant members of the rodent community such as *P. eremicus, R. megalotis,* and *N. macrotis.*

Implications.–Despite fire suppression efforts and management plans, large and small wildfires continue to occur from both natural ignition sources and those associated with increasing human population (Keeley et al. 2004). By understanding the responses of rodent species to fire according to their habitat, nesting, and food preferences, our findings can help managers to identify those species at risk of population decline or extirpation from wildfires, as well as to predict responses of unstudied species.

The spatial extent, severity, and frequency of wildfires are important for determining future risk to rodent species and populations (Shaffer and Laudenslayer 2006). Smaller, patchy, less severe wildfires may allow more species to survive while also leaving some portions of the vegetation intact. These types of fires occurring at natural intervals should allow the persistence of a diverse rodent community and improve the likelihood that impacted areas will recover quickly. Currently, however, most fires are ignited by manmade sources during fall when dry Santa Ana winds act to spread the flames quickly. These large and intense fires increase mortality and more drastically alter wide swaths of habitat. As a consequence, they are more likely to have a greater and more sustained impact on rodent communities. Additionally, a future scenario of more frequent fires increases the potential that large amounts of coastal sage scrub and chaparral habitat may be converted into grasslands (Zedler et al. 1983). The resultant simplified grassland habitat would only be suitable for a much smaller suite of rodent species.

At this time, we are trying to assess whether current habitat conservation plans (HCPs) in southern California provide long term protection to covered species, as well as preserve ecosystem function. Federal and state laws currently require that HCPs be implemented within an adaptive management framework. This framework represents an iterative approach, where an information feedback loop between monitoring and management improves understanding of species dynamics and ecological systems (Atkinson et al. 2004). The future scenario of increased wildfires must be incorporated into this framework (Regan et al. 2008). This will likely require creativity in implementing fire minimization measures, creating of fire safe refugia in natural areas, and working with local and state firefighting agencies to include plans for defense of sensitive natural areas.

The scenario of large and more frequent wildfires may also add a new dimension to the Single Large or Several Small (SLOSS) debate about reserve design and the conservation of biodiversity in this region (Diamond 1975, Simberloff and Abele 1976). Although larger reserves should conserve more species and be less affected by habitat fragmentation, these reserves are more difficult to defend from wildfires. In contrast, smaller reserves within city boundaries may be more likely to be defended as part of firefighting efforts to defend homes in urban and rural areas. A combination of approaches is likely needed.

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FIGURE LEGENDS

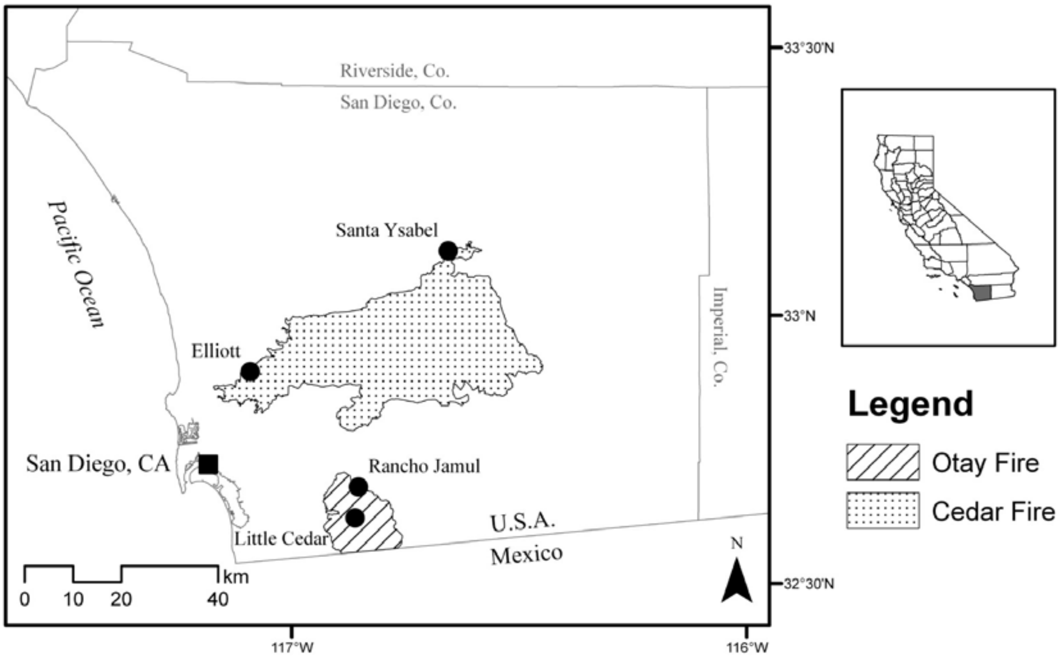

FIG. 1.–The four study sites in San Diego, CA, were Little Cedar Ridge (Little Cedar), Elliott Chaparral Reserve (Elliott), Rancho Jamul Ecological Reserve (Rancho Jamul), and Santa Ysabel Open Space Preserve (Santa Ysabel).

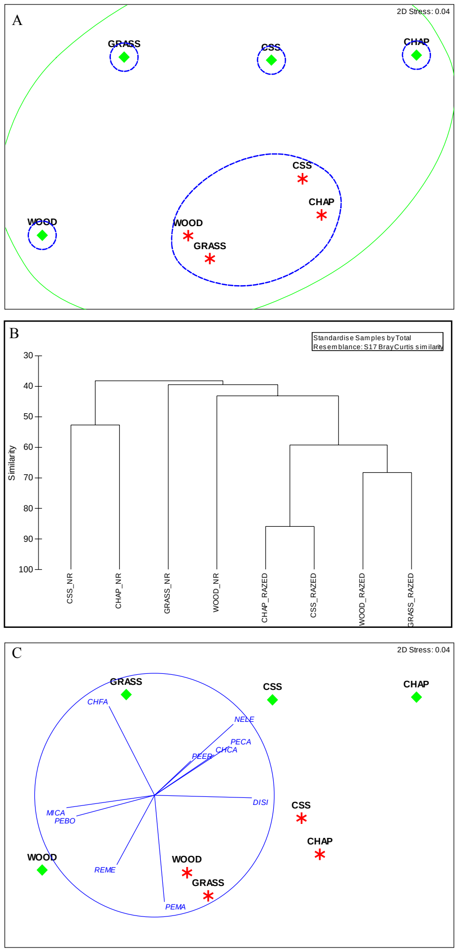

FIG. 2. –Multivariate Community Analysis. A) Nonmetric multi-dimensional scaling (MDS) with B) hierarchical clustering show how the rodent communities in razed plots (R) of coastal sage scrub (CSS), chaparral (CHAP), grassland (GRASS), and woodland (WOOD) have shifted away from the communities detected in the nonrazed plots (NR). C) Vectors of individual species abundances in relation to the razed (*) and nonrazed (◊) communities showed positive responses for both *Peromyscus maniculatus* (PEMA), and *Dipodomys simulans* (DISI) toward the fire impacted communities, while *Peromyscus californicus* (PECA), *Peromyscus boylii* (PEBO), *Chaetodipus fallax* (CHFA), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Chaetodipus californicu*s (CHCA), *Peromyscus eremicus* (PEER) vectors s showed positive responses toward nonrazed communities.

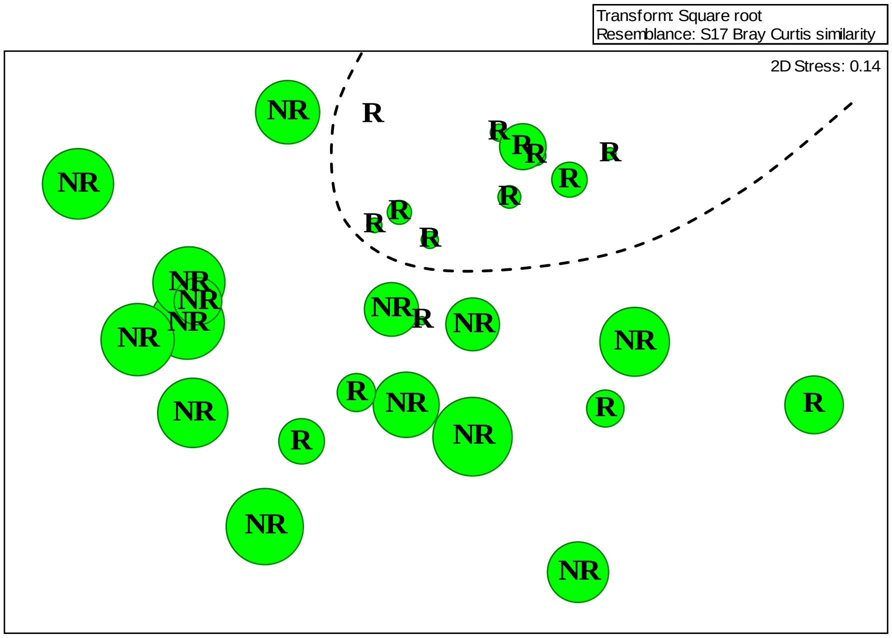

FIG. 3.–Nonmetric multi-dimensional scaling plots (MDS) show how the rodent communities in razed sample plots (R) of coastal sage scrub have shifted away from the communities detected in the nonrazed sample plots (NR). Bubble size corresponds to the relative cover from shrubs and trees. Reduced cover was a significant predictor of the change in rodent community composition in razed plots.

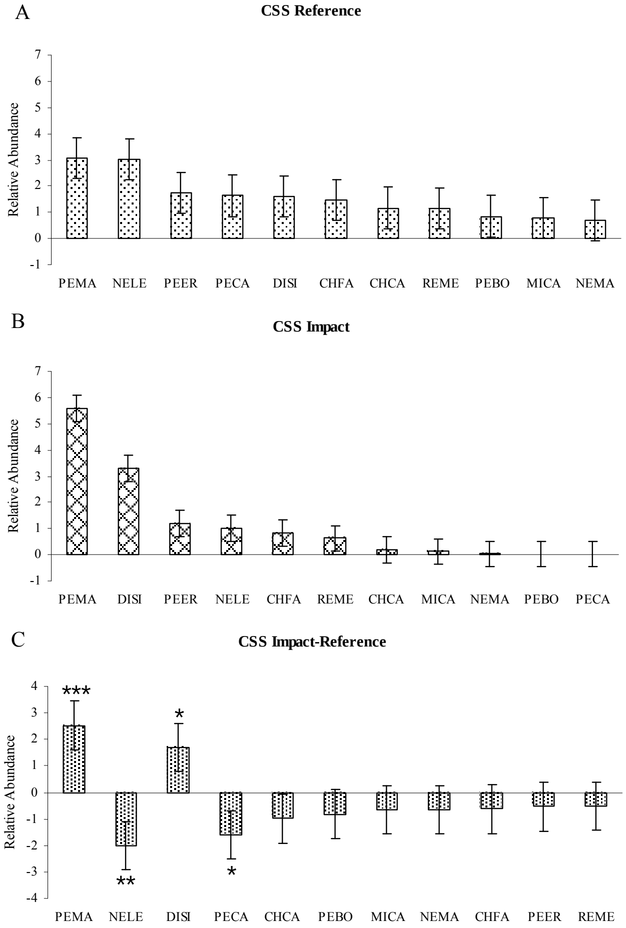

FIG. 4.–Relative abundance of rodent species from postfire surveys in reference (A) and impact (B) plots in coastal sage scrub (CSS) communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in postfire CSS communities are presented in the order of greatest change to smallest change. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are *Chaetodipus californicus* (CHCA), *Chaetodipus fallax* (CHFA), *Dipodomys simulans* (DISI), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Neotoma macrotis* (NEMA), *Peromyscus boylii* (PEBO), *Peromyscus californicus* (PECA), *Peromyscus eremicus* (PEER), *Peromyscus maniculatus* (PEMA) and *Reithrodontomys megalotis* (REME).

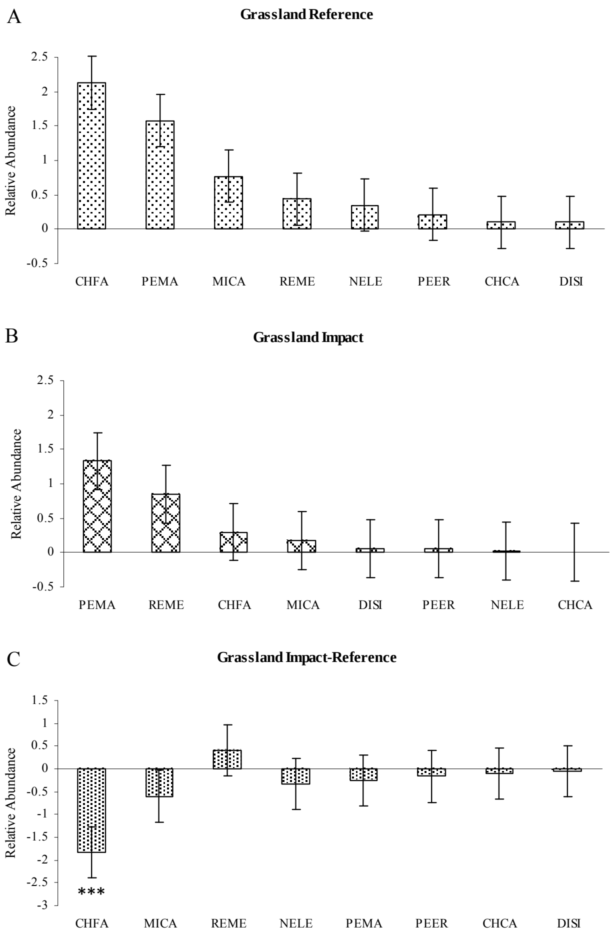

FIG. 5.–Relative abundance of rodent species from postfire surveys in reference (A) and impact (B) plots in grassland communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in postfire grassland communities are presented in the order of greatest change to smallest change. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are *Chaetodipus californicus* (CHCA), *Chaetodipus fallax* (CHFA), *Dipodomys simulans* (DISI), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Peromyscus eremicus* (PEER), *Peromyscus maniculatus* (PEMA) and *Reithrodontomys megalotis* (REME).

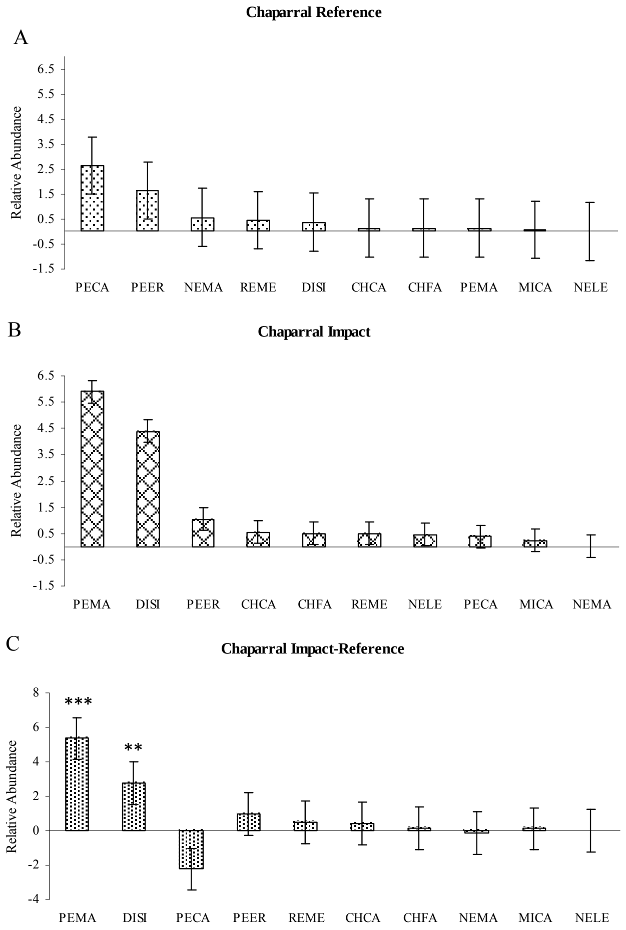

FIG. 6.–Relative abundance of rodent species from postfire surveys in reference (A) and impact (B) plots in chaparral communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in postfire chaparral communities are presented in the order of greatest change to smallest change. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are *Chaetodipus californicus* (CHCA), *Chaetodipus fallax* (CHFA), *Dipodomys simulans* (DISI), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Neotoma macrotis* (NEMA), *Peromyscus californicus* (PECA), *Peromyscus eremicus* (PEER), *Peromyscus maniculatus* (PEMA) and *Reithrodontomys megalotis* (REME).

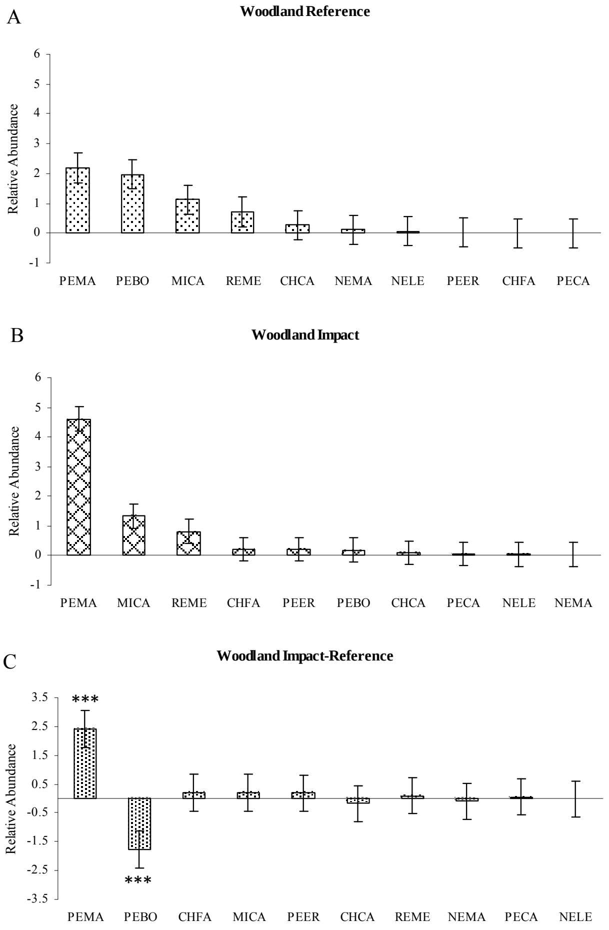

FIG. 7.–Relative abundance of rodent species from postfire surveys in reference (A) and impact (B) plots in woodland communities. Species are ordered from most abundant to least abundant. C) Species differences in relative abundance (impact minus reference) in postfire woodland communities are presented in the order of greatest change to smallest change. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are *Chaetodipus californicus* (CHCA), *Chaetodipus fallax* (CHFA), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Neotoma macrotis* (NEMA), *Peromyscus boylii* (PEBO), *Peromyscus californicus* (PECA), *Peromyscus eremicus* (PEER), *Peromyscus maniculatus* (PEMA) and *Reithrodontomys megalotis* (REME).

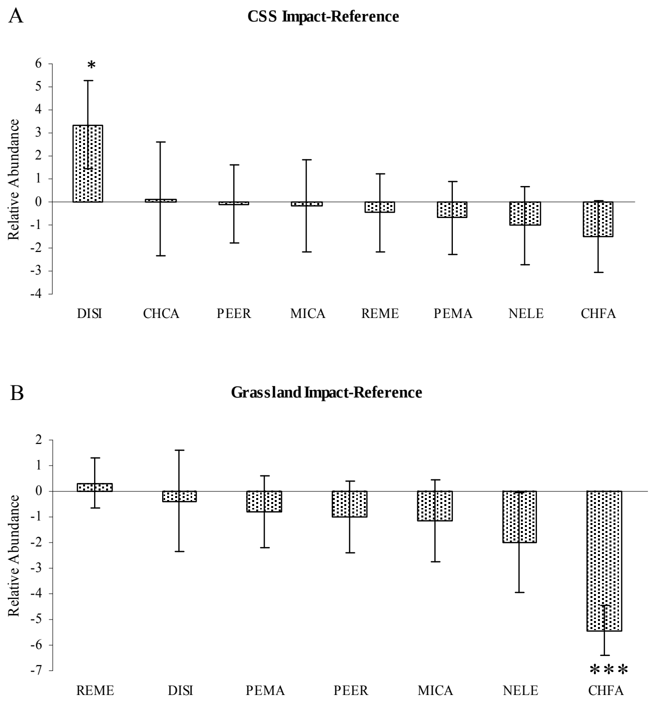

FIG. 8.–Difference in relative abundance (impact minus reference) of rodent species from surveys of impact and reference plots in Rancho Jamul coastal sage scrub (CSS) and grassland community. Levels of significance are indicated as follows: *** $P < 0.01$, ** $P < 0.05$, * $P < 0.10$. Species codes are *Chaetodipus californicus* (CHCA), *Chaetodipus fallax* (CHFA), *Dipodomys simulans* (DISI), *Microtus californicus* (MICA), *Neotoma lepida* (NELE), *Peromyscus eremicus* (PEER), *Peromyscus maniculatus* (PEMA) and *Reithrodontomys megalotis* (REME).

TABLES

	Site						
	Cedar	Elliott	Rancho Jamul		Santa Ysabel		
	Impact	Impact	Reference	Impact	Reference	Impact	
Vegetation Type	NR (R)	NR (R)	NR	NR (R)	NR	NR (R)	Total
Chaparral	0 (5)	0 (5)	0 (0)	0 (0)	0 (2)	0 (4)	0 (16)
Coastal Sage Scrul	0 (4)	0 (5)	4 (4)	4 (4)	0 (2)	0 (2)	8 (21)
Grassland	0 (0)	0 (0)	4 (4)	4 (4)	0 (2)	0 (1)	8 (11)
Woodland	0 (0)	0 (0)	0 (2)	0 (2)	0 (4)	0 (7)	3 (15)
Total	0 (9)	0 (10)	8 (10)	8 (10)	0 (10)	0 (14)	16 (63)

TABLE 1.–Number of impact and reference plots sampled by study site and vegetation type. Impact refers to all plots burned in the 2003 fires. Reference refers to all plots not burned in the 2003 fires. Data are presented as number of plots sampled before the fire followed by number of plots sampled after the fire in brackets. For multivariate analysis, NR (nonrazed) refers to all unburned plots (prefire and postfire reference and prefire impact). R (razed) refers to all burned plots (postfire impact). Both the Elliott and Cedar sites burned completely and thus do not contain reference plots. We collected preburn data at Rancho Jamul only.

Vegetation Type	Cover Type	Percent Cover of Vegetation			
		Postfire		Prefire	
		Reference	Impact	Reference	Impact
		NR	R	NR	NR
CSS	Forb	37.9 (8.1)	69.2 (6.8)	N/A	N/A
	Grass	47.9 (9.5)	54.3 (9.8)	33.0 (7.0)	30.3 (8.6)
	Shrub	59.7 (6.8)	17.3 (6.7)	59.3 (10.1)	72.0 (1.3)
	Tree	0 (0.0)	1.2 (1.4)	0 (0)	0 (0)
GRASS	Forb	70.1 (6.1)	62.1 (9.7)	N/A	N/A
	Grass	76.8 (8.8)	89.9 (3.4)	79.0 (6.6)	90.4 (2.4)
	Shrub	2.1 (1.3)	2 (1.7)	0.8 (0.0)	8.4 (5.6)
	Tree	0 (0)	0 (0)	0.2 (0.2)	0 (0.0)
CHAP	Forb	48.3 (14.3)	42.9 (5.5)	N/A	N/A
	Grass	37.5 (7.9)	28.2 (6.5)	N/A	N/A
	Shrub	63.3 (3.6)	33.9 (4.8)	N/A	N/A
	Tree	0 (0)	0 (0)	N/A	N/A
WOOD	Forb	53.6 (12.3)	55.4 (5.9)	N/A	N/A
	Grass	84.8 (5.7)	67.5 (7.3)	N/A	N/A
	Shrub	5.5 (3.6)	7.4 (4.6)	N/A	N/A
	Tree	11.7 (6.1)	12.9 (5.1)	N/A	N/A

NR = Nonrazed plots
R = Razed plots

TABLE 2.–Means and standard errors for the percent cover of forbs, grass, shrubs and trees over reference and impact plots for coastal sage scrub (CSS), chaparral (CHAP), grassland (GRASS), and woodland (WOOD). Postfire reference and impact plots were sampled at all four sites. Prefire refers to eight CSS and eight GRASS plots sampled before the fire at the Rancho Jamul site only. Prefire forb cover is not presented as prefire vegetation surveys were conducted in the fall when most forbs are dry and disarticulated.

	Habitat and Dietary Preferences[a]			Study Results		
Species	Diet	Nesting	Microhabitat Use	Other Studies	Current Study	Reference[b]
Chaetodipus californicus	Grass/forb specialist	Below ground	Ground	N/A	N.S.	N/A
Chaetodipus fallax	Grass/forb specialist	Below ground	Ground	$D^{S}I^{C}$	D^{G}	3, 6
Dipodomys simulans	Grass/forb specialist	Below ground	Ground	$I^{S,C}$	$I^{S,C}$	1-3, 5-6
Microtus californicus	Grass/forb specialist	Below ground	Ground	$I^{G,S,C}$	N.S.	1-3, 5-6
Neotoma lepida	Shrub specialist	Above ground	Shrub	$D^{S,C}$	D^{S}	1-3, 5-6
Neotoma macrotis	Shrub specialist	Above ground	Shrub	$D^{S,C}$	N.S.	1-3, 5-6
Peromyscus boylii	Shrub specialist	Below ground	Shrub	N/A	D^{W}	4
Peromyscus californicus	Shrub specialist	Above ground	Shrub	$D^{G,S,C}$	$D^{S,C}$	1-3, 5-6
Peromyscus eremicus	Shrub specialist	Below ground	Shrub	D^{S}	N.S.	1, 3, 5
Peromyscus maniculatus	General	Below ground	Ground	$I^{G,S,C}$	$I^{S,C,W}$	1-3, 5-6
Reithrodontomys meglotis	General	Above ground	Ground	$I^{G,S,C}$	N.S.	1-3, 5-6

[a] Natural history references: Cook 1959; Grinnell and Orr 1934; Holbrook 1978; Jameson 1952; Jameson and Peeters 2004; Lackey 1996; M'Closkey 1972; Merritt 1974; Meserve 1976a, 1976b; Price and Waser 1984; Stark 1963; Verts and Carraway 2002.

[b] Study result references: Cook 1959[1]; Lawrence 1966[2]; Price et al. 1995[3]; Roberts et al. 2008[4]; Schwilk and Keeley 1998[5]; Wirtz et al 1988[6].

TABLE 3.–A summary and review of rodent species habitat and dietary preferences and responses to fire reported in other studies. (I) indicates the species increased in abundance after fire, (D) indicates species decreased in abundance after fire, (N.S.) indicates no significant response to fire. Vegetation types of reported responses are indicated as a superscript as follows:chaparral^{C}; grassland^{G}; coastal sage scrub^{S}; woodland^{W}.