

## Fire as a Management Tool for Stephens' Kangaroo Rat and Other Small Mammal Species

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**Abstract.** Active management of habitat plays an essential role in the conservation of endangered wildlife when native habitat is rare and fragmented, as is the case in southern California. Any successful management plan in this region must incorporate fire, an ancestral element of native ecosystems. Fire has direct effects on wildlife populations, which may be beneficial or neutral but usually are harmful; and also much longer-term indirect effects through changes in habitat characteristics. Depending on their natural histories, wildlife species will respond to fire with local population increases or decreases that are predictable *a priori*. We illustrate this point, and its value for management, with two examples. In the first, we experimentally confirmed a prediction that a controlled fire would increase population density of the endangered Stephens' kangaroo rat (*Dipodomys stephensi*) in annual grassland vegetation. In the second, we used knowledge of species-specific microhabitat affinities to predict long-term changes in the relative abundances of four small mammal species following a wild fire in coastal sage scrub vegetation. The predictability of long-term fire effects suggests that controlled fires which result in a mosaic of habitat features will be valuable for maintaining high species diversity in habitat fragments.

**Keywords:** Annual grassland; biodiversity; *Chaetodipus*; coastal sage scrub; conservation; *Dipodomys agilis*; *Dipodomys stephensi*; endangered species; fire; long-term management; *Peromyscus*.

### Introduction

Loss or alteration of habitat is a major cause of anthropogenic extinctions. When abundant suitable habitat is available, a threatened species often persists without intervention, but when habitat is rare and fragmented, extinction may only be avoided through wise management of what remains.

Southern California is a case in point. Its natural habitats continue to be lost and fragmented by human activity, placing a growing list of native animals and plants at risk of extinction. To safeguard these species we must do two things. First, we must preserve the habitat that remains. Second, we must develop strategies to manage remaining habitat fragments effectively, so as to maintain or enhance their quality from the perspective of endangered species. Fire, an ancestral force in the mediterranean ecosystems of the region, is a critical component of any effective management strategy.

From the perspective of native animals, fire exerts both direct and indirect effects (Fig. 1). Direct effects are transient, occurring on a scale of minutes to days. Usually they are negative: individuals are killed outright, or their food supplies or nest sites are destroyed. However, direct effects on some species are negligible, because individuals can endure the fire in protected microsites or are mobile enough to escape flames, heat, and smoke. Also, for some species, fire can actually yield an immediate, albeit temporary, increase in food availability. In contrast, indirect fire effects are long-term, occurring on a scale of months to years, and come about through changes in habitat characteristics such as primary productivity, plant species composition, and physical structure. Such changes can be detrimental or beneficial to a given wildlife species depending on its habitat affinities, which in turn result from ecological attributes such as reproductive requirements, food habits, and foraging.

In designing fire management strategies to maintain or improve the quality of a given habitat from a wildlife perspective, we should not underestimate the value of a solid knowledge of natural history. With this knowledge in hand for the wildlife species of interest, and with knowledge of how fire will alter vegetation characteristics, we often can predict what a particular management strategy will achieve. In what follows, we illus-

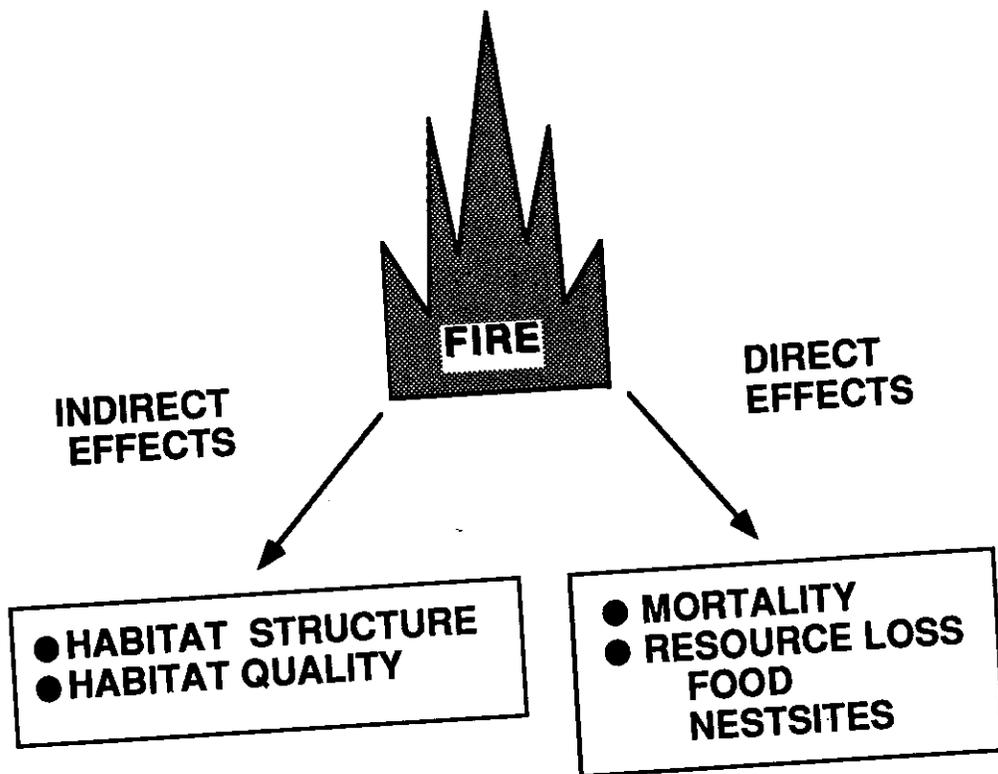


Figure 1. Direct and indirect mechanisms by which wildfire can affect wildlife populations.

trate this point with two examples. In the first example, we predict how fire will influence population density of an endangered kangaroo rat and test our predictions with experimental fires in annual grassland vegetation. In the second example, we use prior knowledge of species-specific affinities for different structural habitat features to forecast successfully how the relative abundances of four native small mammal species change over a long period in response to wildfire in coastal sage scrub vegetation.

#### Fire and Habitat Management for Stephens' Kangaroo Rat

Stephens' kangaroo rat (*Dipodomys stephensi*) is a nocturnal, burrowing rodent in the family Heteromyidae. Like other kangaroo rat species, it eats mostly seeds (Lowe 1993) that it harvests from low-growing plants or from the soil surface after seeds have been dispersed from plants. Harvested seeds are subsequently buried either in the underground burrow or in shallow caches

on the soil surface (Reichman and Price 1993). The geographical range of the species comprises approximately 287,000 ha in western Riverside, northern San Diego, and southern San Bernardino counties, California (Bleich, 1977, Kramer 1987, Price and Endo 1989). Within its range, Stephens' kangaroo rat reaches highest densities in flat to gently sloping annual grassland habitat with low vegetation cover and a high abundance of prostrate forbs relative to grasses (O'Farrell and Uptain 1987, 1989). In such habitats, individuals occupy non-exclusive home ranges of about 1,000 m<sup>2</sup> (Kelly and Price 1992) and reach densities at least as high.

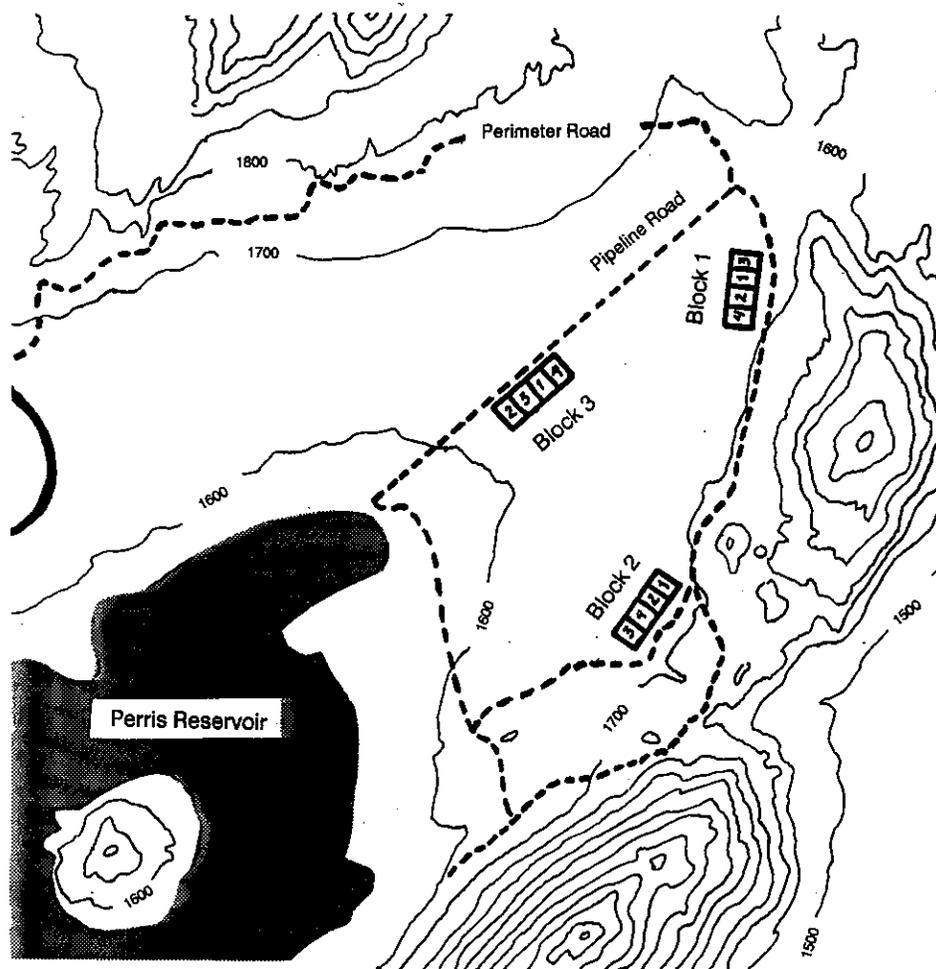
Because Stephens' kangaroo rat occupies a habitat suited for agricultural and urban development, human population growth in southern California has resulted in extensive habitat loss and fragmentation, and the species is at risk of extinction (Goodman 1987, Gilpin 1987, Price and Endo 1989). The State of California characterized Stephens' kangaroo rat as threatened in 1973 (Leach and Fisk 1972), and the United States listed the species in 1988 under the Endangered Species Act (Kramer 1987, 1988).

In accordance with its Resource Management Directives, the California Department of Parks and Recreation undertook to develop a management strategy for Stephens' kangaroo rat on its lands. One goal was to assess the potential of controlled fire to enhance habitat for the species. We predicted that Stephens' kangaroo rats would be buffered from direct harmful effects of fire because individuals live underground and bury their food. Furthermore, to the extent that fire reduces vegetation cover and favors prostrate forbs over grasses, we predicted that indirect effects would favor the animals. We tested these predictions by monitoring kangaroo rat population densities and vegetation on a series of unburned and experimentally burned plots (see also Price 1993, Price and Taylor 1993).

### Methods

*The study area and plot design.* The study area was in the Lake Perris State Recreation Area, Riverside County, California, within a broad basin containing the reservoir and bordered by low granitic hills (Fig. 2). This basin varies from 216 to 583 m elevation with 0-15% slopes. The area is well suited for controlled fires because a dirt perimeter road acts as a fire break. An additional dirt "Pipeline Road" bisects the basin; our study was conducted south of this track.

Three rectangular blocks, each measuring 150 x 180 m (2.7 ha), were placed in representative regions of the study area (Fig. 2). Each block was divided into four plots measuring 45 x 150 m (0.68 ha), and each plot was randomly assigned to receive one of four treatments: (1) burned December 1990; (2) burned May 1991; (3) burned October 1991; (4) unburned control.



**Figure 2.** Map of the study area in the Lake Perris State Recreation Area. Numbers within three study blocks indicate fire treatments: 1 = burned December 1990; 2 = burned May 1991; 3 = burned October 1991; 4 = unburned control. Dashed lines denote dirt roads; thin solid lines indicate 100-foot contour intervals.

**Vegetation of the study area.** Most of the study area is classified as European annual grassland (Heady 1977, O'Farrell and Uptain 1989), some of which was cultivated until the recreation area was established in 1973. Vegetation cover increases from the periphery (blocks 1 and 2) to the center of the basin (Block 3). Dominant herbaceous species were *Bromus diandrus* (ripgut brome), *B. madriensis* (red brome), *Avena fatua* (wild oats), *A. barbata* (slender oats), *Schismus barbatus* (Mediterranean schismus), *Hirschfeldia incana* (wild mustard), *Erodium cicutarium* (filaree), *Lasthenia californica* (goldfields), *Lupinus bicolor* (lupine), and *Amsinckia menziesii* (fiddleneck). Cover of woody species is negligible.

**Stephens' kangaroo rat censuses.** A permanent 3- by 12-station live-trapping grid with 10 m spacing between adjacent stations was established in each plot. During rodent censuses a single live-trap was placed at each station.

There were two types of census (Table 1). First, three "incomplete" censuses of two plots per block were conducted before and immediately after each controlled fire, to determine whether more kangaroo rats disappeared immediately from burned than from unburned sites. Second, five "complete" censuses of all four plots per block were conducted in August 1990, May 1991, August 1991, October 1991, and March 1992. For either type of census, we monitored plots within a block simultaneously for three consecutive nights each. During incomplete censuses, all three blocks were monitored simultaneously. Because controlled fires were not consistently performed at any given moon phase, incomplete censuses occurred randomly with respect to moon phase. During complete censuses, we sampled blocks on three consecutive three-night periods centered around the new moon.

During censuses, traps were opened at dusk and baited with mixed birdseed. They were either checked twice per night at six-hour intervals, or (during espe-

cially cold nights) were checked at midnight and closed for the rest of the night. We did not open traps when rain was predicted.

Captured kangaroo rats were weighed to the nearest gram and their sex and reproductive condition were noted. Each captured kangaroo rat was individually marked with a numbered fingerling ear-tag and released. All other captured rodent species were identified to species and released.

Kangaroo rat abundance on each plot was expressed as the minimum number known alive. This method counts an animal as alive at a given census date, even if it is not encountered in that census, so long as it is caught in earlier and later censuses; the method works well when plots are small and animals readily enter traps, as was true here (Hilborn et al 1976, McClenaghan and Taylor 1993).

**Estimates of kangaroo rat activity.** Stephens' kangaroo rat populations were not censused directly by live-trapping in April 1993. Instead, we recorded the number of active burrows within a 1 m-wide belt transect along the midline of each plot. Active burrow density is highly correlated with population densities measured by live-trapping (O'Farrell and Uptain 1989, Eller and Price 1990).

**Soil seed bank censuses.** Direct effects of fire on the soil seed bank were assessed by counting seeds contained in surface soil samples taken from burned plots immediately before and after fires. Six soil samples, each 6.5 cm in diameter and 6.75 cm deep, were taken from each May 1991 and October 1991 treatment plot before the scheduled fire, and six more were taken after the fire. Samples were sifted through sieves with 2.00 and 0.42 mm openings. The 2.00 mm fraction was inspected visually for seeds. Organic material was extracted from the 0.42 mm fraction and sorted as described in Price and Reichman (1987). Filled seeds were counted and scored as either viable or charred.

**Vegetation censuses.** Vegetation on each plot was measured in summer 1990 (before any fires), and in spring 1992 and 1993 (after all fires). We arranged sample areas every 10 m along a line transect that traversed the long axis of each plot. A 0.5 x 0.5 m quadrat divided into 100 5 x 5 cm squares was placed over each sample area and percentage cover of each of three vegetation categories was estimated by counting the number of squares occupied by  $\geq 50\%$  of each category. The categories were: bare ground, tall vegetation ( $\geq 30$  cm high), and short vegetation ( $< 30$  cm high). In addition, we estimated the frequencies of four taxa (*Erodium cicutarium*, *Amsinckia intermedia*,

Table 1. Schedule of Stephens' kangaroo rat censuses conducted on the three Lake Perris study blocks. "X" indicates that a plot was trapped for three nights during a particular census period; "last" = last quarter moon; "first" = first quarter moon.

Census Date	Control	Burn Date			Moon
		Dec 90	May 91	Oct 91	
16-25 Aug 90	X	X	X	X	new
15-17 Dec 90	X	X	X	X	new
11-20 May 91	X	X	X	X	full
1-4 Jun 91	X	X	X	X	last
5-13 Aug 91	X	X	X	X	last
28 Sep-1 Oct 91	X	X	X	X	last
30 Oct-7 Nov 91	X	X	X	X	first
11-18 Mar 92	X	X	X	X	

*Bromus* spp., and *Avena* spp.) by counting the number of squares out of 100 that each taxon occupied. We also recorded maximum stem height for each quadrat in 1990 and 1992 censuses.

**Controlled fires.** The entire study area was burned on 13 December 1990, except for the three plots per block scheduled to be burned in May or October 1991 or to remain unburned. Subsequent fires, on 28 May 1991 and 9 October 1991, involved only one plot per block. All three fires were administered jointly by the Department of Parks and Recreation and the Department of Forestry and Fire Protection.

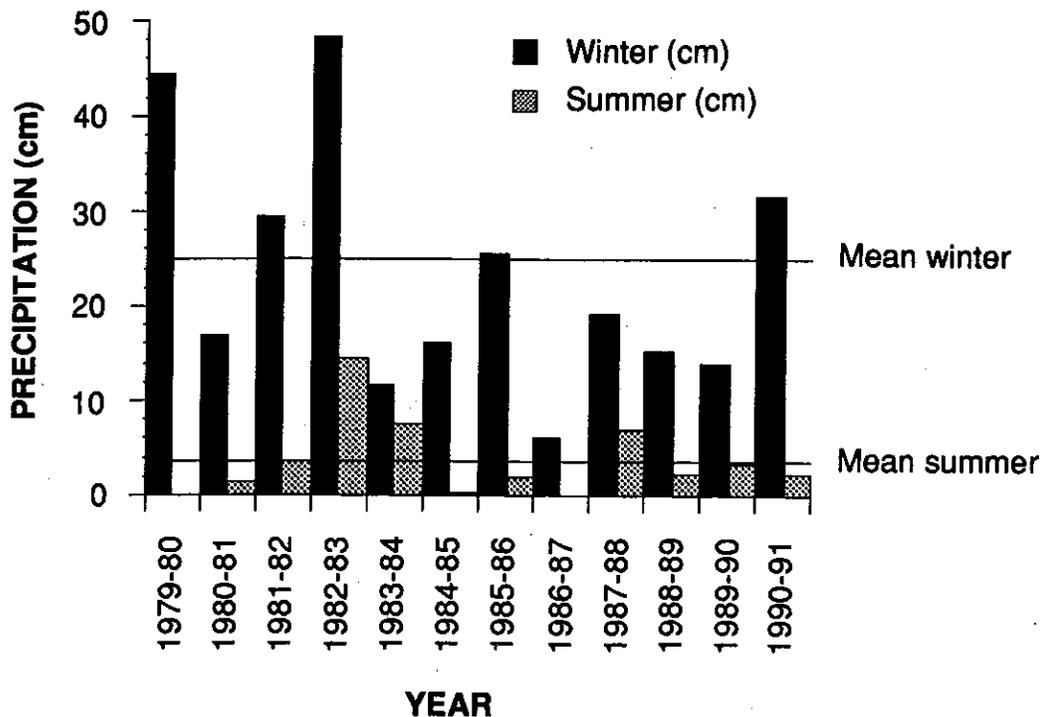
The December 1990 fire had a low fuel load because it followed several years of subnormal winter rainfall (Fig. 3). Its intensity was estimated as 624 BTU m<sup>-2</sup> by BEHAVE, a fire model developed by the Northern Forest Fire Laboratory (Albini 1976). More fuel was available in May 1991 after heavy rains of March 1991, and the fire intensity was estimated as 1001 BTU m<sup>-2</sup>. The October 1991 fire occurred after the prior season's growth had dried and during lower relative humidity than the other two fires, and its intensity was estimated as 9827 BTU m<sup>-2</sup>.

**Results and Discussion**

*Short-term effects of fire on Stephens' kangaroo rat and its habitat.* Fires had no immediate effect on survival of Stephens' kangaroo rats. The likelihood that an individual present in a pre-fire census would subsequently disappear, was equivalent for burned and control plots in the same block (paired t-test:  $t = -0.35$ , d.f. = 8,  $P = 0.75$ ). Of 48 kangaroo rats captured on burned plots in pre-fire censuses, 13 (27%) were never recaptured after burning, compared to 10 of 40 animals (25%) on control plots.

As expected, fire also had no effect on seeds available to kangaroo rats (Table 2). There was no significant decline in densities of viable seeds after the fires (no time effect in a repeated-measures ANOVA;  $F = 0.20$ ,  $P = 0.66$ ), and the fraction of charred seeds was small, on the order of 10%.

*Long-term effects of fire on Stephens' kangaroo rat and its habitat.* Based on the number of Stephens' kangaroo rats known alive during each complete census (Table 3), the three blocks supported significantly different densities of animals in the first census (Au-



**Figure 3.** Total winter (October - March) and summer (April - September) precipitation recorded at the Riverside Fire Station #3 weather station from 1979 - 1991. Each time interval starts with October of the first year and ends with September of the second year. For example, winter precipitation for the 1979-80 period is total precipitation from October 1979 through March 1980, and summer precipitation for the 1979-80 period is total precipitation from April 1980 through September 1980.

Table 2. Effect of fire on densities of seeds in the soil in the Lake Perris study. Densities, expressed as the number of seeds per 1 m<sup>2</sup> area, are based on numbers of viable or charred seeds extracted from soil samples (6.5 cm in diameter and 6.8 cm deep) collected immediately before and immediately after the controlled fires of May and October 1991. SD = standard deviation; N = number of samples.

	Before Fire		After Fire			
	Viable Seeds/m <sup>2</sup>		Viable Seeds/m <sup>2</sup>		Charred Seeds/m <sup>2</sup>	
	May	Oct	May	Oct	May	Oct
Mean	21,999	17,660	17,388	29,021	2,019	3,526
SD	41,949	23,958	34,114	58,554	3,255	5,063
N	18	18	17	18	17	18

gust 1990), before any fires (block effect:  $F_{2,6} = 19.58$ ,  $P = 0.002$ ), but plots designated to receive different fire treatments supported equivalent densities (treatment effect:  $F_{3,6} = 0.04$ ,  $P = 0.99$ ). Thus, the blocks varied in their initial suitability for kangaroo rats, but there were no significant pre-treatment differences among plots within blocks. From May 1991 to the last census in March 1992, kangaroo rat populations grew overall in the study blocks (Table 3), probably as a result of the wet March of 1991 which stimulated seed production. Blocks differed significantly in population growth ( $F_{2,6} = 7.72$ ,  $P = 0.022$ ); the average increases were 22.8, 14, and 16 individuals for blocks 1, 2, and 3, respectively. Stephens' kangaroo rat populations at other locations also grew following March 1991 (Price and Kelly 1994).

To evaluate whether the population increase was greater for some treatments than others, we calculated for each plot the change in number known alive between August 1990 and March 1992 and used ran-

Table 3. Number of Stephens' kangaroo rats known alive on each study plot during five complete censuses. Fractional values occur because some individuals were captured on more than one plot during a census; these individuals were apportioned equally among plots they occupied.

Block	Treatment	Census Date:	Number Alive				
			Aug 90	May 91	Aug 91	Nov 91	Mar 92
1	Control		4.5	2	14	25.8	24.5
	Dec 90 fire		8.5	5	17.5	29.3	28
	May 91 fire		6	1	20	24	36.5
	Oct 91 fire		8	5	14.5	29.8	29
2	Control		8.5	4.5	5.5	17.5	19
	Dec 90 fire		5	3	3.5	10.5	15
	May 91 fire		8.5	5.5	13	18	25
	Oct 91 fire		6	3	3	8	25
3	Control		0	1.5	2	4.5	8.5
	Dec 90 fire		0	0.5	2	7.5	16.5
	May 91 fire		0	1	2	5	23
	Oct 91 fire		0	0	1	5	16

domized-blocks ANOVA to see whether the increase differed among treatments. Indeed, there was a significant treatment effect ( $F_{3,6} = 5.54$ ,  $P = 0.036$ ): plots burned in May 1991 supported almost twice the population growth experienced on paired control plots (an increase in population size by 23.3 individuals on average for burned plots vs. 13.0 for controls), and the difference was highly significant ( $F_{1,6} = 14.71$ ,  $P = 0.009$ ). Neither of the other fire treatments differed significantly from their paired controls ( $P > 0.08$ ), but all the burned plots gained more individuals on average during the study than did their paired controls (18.7 and 15.3 individuals gained on average for October 1991 and December 1990 burned plots, respectively vs. 13.0 for controls).

Stephens' kangaroo rats remained more abundant on burned plots in April 1993, judging from the density of active burrows (Table 4). A randomized-blocks ANOVA indicated that burrow densities were higher on May 1991 and October 1991 plots than on unburned controls ( $F_{1,6} = 13.67$ ;  $P = 0.01$ ).

Table 4. Abundance of active burrows of Stephens' kangaroo rats on each of four burned treatments during April 1993. Active burrows were scored in a 1 m x 150 m belt transect down the midline of each study plot. Values are means and standard deviations (SD) across three replicate blocks. Asterisks indicate values significantly different from unburned controls at or below the 5% level, from randomized-blocks ANOVA.

	Unburned Control	Active Burrows		
		Burn date : Dec 90	May 91	Oct 91
Mean	6.7	12.3	22.0*	22.0*
SD	5.5	7.2	10.1	12.1

As predicted, the long-term benefit of fire to kangaroo rats seems to occur through an increase in bare ground with a minimal effect on prostrate forbs. In summer 1990, before any fires, there were no significant differences among treatments in the amount of bare ground or abundance of the dominant prostrate forb *Erodium cicutarium* (Table 5). However, in spring 1992 burned plots had more bare ground than unburned controls (Table 5), and the effect was significant for the May 1991 fire treatment, although not for the December 1990 or October 1991 treatments. Plots burned in May 1991 also had greater frequency of *Erodium cicutarium*, although the effect was not statistically significant. These trends continued to the April 1993 census (Table 5). In addition, the abundance of Stephens' kangaroo rats was correlated positively across the 12 study plots with the amount of bare ground in both the August 1990 and March 1992

**Table 5.** Results of vegetation censuses in the Lake Perris study. The August 1990 census occurred before any fires; the May 1992 and April 1993 censuses occurred after all three controlled fires. Values are means and standard deviations (across blocks) of treatment plot means for two vegetation variables. Plot means are based on 20 sample quadrats per plot. "Type" refers to the type of variable; "% cover" indicates the number of 5 x 5 cm quadrat squares (out of 100) with >50% of a particular cover category; "Freq." = number of 5 x 5 cm quadrat squares occupied by at least one individual of a taxon; "SD" = standard deviation. Asterisks indicate variables significantly different from controls at or below the 5% level, from randomized-blocks ANOVA.

Variable	Type	Vegetation Cover and Frequency				
		Control	Burn Date: Dec 90	May 91	Oct 91	
<b>August 1990 Census</b>						
Bare Ground	% cover	Mean	37.8	37.8	37.0	48.1
		SD	28.1	27.7	32.3	32.3
<i>Erodium cicutarium</i>	Frequency	Mean	30.1	27.0	25.6	29.7
		SD	10.8	16.1	15.8	3.4
<b>May 1992 Census</b>						
Bare Ground	% cover	Mean	19.0	20.3	47.2*	28.0
		SD	8.8	7.2	3.7	5.5
<i>Erodium cicutarium</i>	Frequency	Mean	61.0	60.8	73.6	59.2
		SD	3.4	11.2	23.9	2.7
<b>April 1993 Census</b>						
Bare Ground	% cover	Mean	5.9	11.1	19.7*	20.4*
		SD	13.8	13.3	15.4	23.1
<i>Erodium cicutarium</i>	Frequency	Mean	6.0	9.9	12.1	9.6
		SD	5.3	11.1	13.3	7.6

censuses ( $r = 0.86$ ,  $P = 0.0003$  and  $r = 0.62$ ,  $P = 0.33$ , respectively).

We conclude that fires, especially those that occur in late spring after forbs have shed seeds but before annual grasses have shed seeds, have no direct detrimental effects on Stephens' kangaroo rats over the short term. Instead, such fires have a positive effect on kangaroo rat populations that persists for at least two years. This benefit appears to occur because late spring fires are effective in promoting a habitat structure dominated by bare ground and sparse, low-growing forbs, at the expense of plants with upright growth form. This is the structure that currently typifies Stephens' kangaroo rat habitat, and that may have typified the ancestral pre-European habitat as well.

#### Postfire Response of a Coastal Sage Scrub Rodent Community

The Stephens' kangaroo rat study indicates that fire can be a valuable tool for managing a single species of concern and that natural history information leads to accurate expectations about short- and long-term consequences of fire. Our second example illustrates that the same logic permits qualitatively accurate predictions about effects of fire on an entire assemblage of rodent species. Price and Waser (1984) detail results from the first 2.5 years after the fire; here we extend the results to 10.5 postfire years.

#### Methods

**Study site and fire history.** In September 1979, an arson fire burned much of the University of California's Motte Rimrock Reserve, a 7200-ha granitic outcrop at 550 m elevation situated 24 km south of Riverside, California. One boundary of the fire traversed a topographically uniform area near the northern edge of the reserve. From prefire censuses, we know that the perennial vegetation on either side of this fire boundary was homogeneous coastal sage scrub before the fire (F. Vasek, personal communication). Dominant shrubs were *Salvia mellifera* and *Eriogonum fasciculatum*, and the understory consisted of exotic annual grasses (*Bromus* and *Schismus* species) and exotic and native forbs such as *Erodium cicutarium* and species of *Plagiobothrys*, *Lasthenia*, and *Camissonia*.

**Census methods.** In January 1980, four months after the fire, we established a permanent 100-station grid across the fire boundary. The grid consisted of five lines 15 m apart, with stations spaced every 10 m along each line. Each line contained 9-10 stations in unburned vegetation and 10-11 stations in the burned area. The rodent community and vegetation on the grid were censused regularly until a second fire swept through the area in 1991.

During rodent censuses, we placed two live-traps 1 m apart at each grid station, and trapped within the grid for three non-consecutive nights, for a total of 600 trap-

nights per census. Rodents were first censused in January 1980, and approximately yearly thereafter, in late autumn or early winter. The last census occurred in January 1991. Traps were opened and baited with rolled oats or mixed birdseed in late afternoon and were checked and closed at 0600 the next morning. Captured animals were toe-clipped or ear-tagged for individual recognition. We recorded the species, individual number, sex, and station for each capture.

Vegetation structure on the grid was monitored yearly or bi-yearly. The first vegetation census occurred in February 1980 and subsequently in autumn, concurrently with the rodent census. We characterized vegetation structure in terms of the cover of four structural habitat elements, or "microhabitats," that are often distinguished by rodents. The microhabitats were "open" (bare ground devoid of plant cover), "bush" (under the canopy of a live woody perennial shrub), "grass" (standing live or dead herbaceous material), or "debris" (fallen dead woody material). Grass and debris categories were combined in the grass category prior to the November 1982 census, but were distinguished thereafter.

Cover of each microhabitat was quantified with four line transects, each 5 m long, radiating from the center of each station to the points of the compass. We recorded the number of meters of each microhabitat intersected by each transect, and summed the totals over the four transects and divided by 20 m to calculate proportional cover of each microhabitat at each station. Total cover could sum to more than 100% by this method. Vegetation structure was characterized separately for burned and unburned halves of the grid by averaging over appropriate groups of stations.

## Results

*The rodent species.* Four nocturnal, granivorous or omnivorous rodent species were recorded regularly on the study grid: two heteromyid rodents (the Pacific kangaroo rat, *Dipodomys agilis*, and San Diego pocket mouse, *Chaetodipus fallax*) and two cricetids (the cactus mouse, *Peromyscus eremicus*, and deer mouse, *Peromyscus maniculatus*). Price and Waser (1984) and Price and Kramer (1984) describe the microhabitat affinities of these species, as measured by their relative frequency of capture when equal numbers of live-traps are placed in each microhabitat category. With this sampling regime, an indiscriminant rodent should be caught equally frequently in all microhabitats (Price and Kramer 1984).

All species except for *P. maniculatus* deviated significantly from a uniform capture frequency (Price

and Kramer 1984). *Dipodomys agilis* specialized on the open microhabitat; *P. eremicus* and *C. fallax* were caught most often in the bush microhabitat (and in rocky areas). *Peromyscus maniculatus* was captured twice as often in debris and grass as in open or bush microhabitats, but the effect was not statistically significant.

Because all four rodent species live in burrows or rock crevices, fire should not directly increase mortality. However, if abundances are determined largely by the availability of preferred microhabitats, we should be able to predict indirect fire effects from knowledge of microhabitat associations and effects of fire on microhabitat availability (Price and Waser 1984).

*Effects of fire on vegetation structure.* Initially, the fire dramatically increased the availability of open microhabitat at the expense of bush, grass, and debris (Fig. 4; Price and Waser 1984). Although vegetation recovered gradually on the burned half of the grid, significant overall differences in vegetation structure remained in 1988 and 1989, 9 to 10 years after the fire occurred (MANOVA: Wilks' lambda = 0.58,  $F_{5,192} = 27.470$ ,  $P = 0.0001$ ). Repeated-measures ANOVA performed on individual microhabitat variables (with treatment effects tested over station nested within treatment) indicated that in the 1988-1989 censuses, burned areas still had significantly more open microhabitat ( $F_{1,98} = 22.033$ ,  $P < 0.001$ ), less bush ( $F_{1,98} = 6.01$ ,  $P < 0.025$ ), less grass ( $F_{1,98} = 9.07$ ,  $P < 0.005$ ), and less debris ( $F_{1,98} = 121.66$ ,  $P < 0.001$ ) than unburned areas (Fig. 4).

*Effects of fire on the rodent community.* Overall rodent densities varied substantially through time (Fig. 5), reflecting temporal variation in rainfall (Fig. 3); the total number of individuals captured during a census was positively correlated with the previous winter's rainfall ( $r = 0.72$ ,  $n = 10$  years,  $P < 0.05$ ). Despite these fluctuations, burned and unburned halves of the grid supported different rodent assemblages. *Dipodomys agilis* and *P. maniculatus* were consistently more abundant on the burned than unburned half of the grid (11 of 12 censuses for *D. agilis*, 9 of 11 censuses for *P. maniculatus*). A nonparametric sign test yielded  $P < 0.033$  in both cases; i.e., these patterns are highly unlikely under the null hypothesis of no difference between burned and unburned halves of the grid. *Peromyscus eremicus* and *C. fallax*, in contrast, were consistently more abundant on the unburned half of the grid (9 of 10 censuses for *P. eremicus* and 10 of 12 censuses for *C. fallax*). A sign test yielded  $P < 0.02$  in both cases.

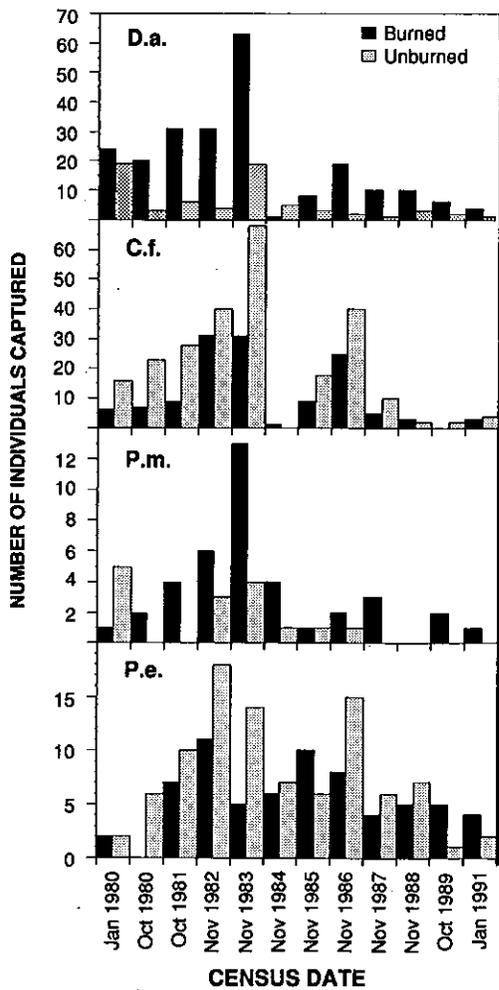


Figure 4. Postfire changes in vegetation structure at the Motte Rimrock Reserve. Bars depict average proportional cover of four structural microhabitats at stations that either were or were not burned in September 1979. Asterisks indicate censuses during which grass and debris microhabitats were not distinguished from one another.

These differences in response to the fire can be predicted from knowledge of microhabitat affinities (Price and Waser 1984). The two species that preferred the bush microhabitat (*P. eremicus* and *C. fallax*) were consistently more abundant on the unburned half of the grid and together comprised 80% (range 44-95% across censuses) of all rodents captured there. Similarly, the two species that preferred non-bush microhabitats (*D. agilis* and *P. maniculatus*) were more abundant in burned habitat and together comprised 55% of the rodent fauna there (range 38-77% across censuses).

Discussion

Our two case histories indicate that populations of small mammal species in southern Californian habitats have a variety of responses to fire, both negative and positive. The most important of these responses are long-term decreases or increases in population density, lasting as long as a decade or more, brought about by fire-induced changes in physical structure of the environment from a mouse's-eye view. In common with other vertebrates (Schoener 1974), small mammals often have distinctive affinities for features of physical structure on a small scale, i.e., for microhabitats (Price 1978). The basis for these affinities is poorly understood, but their effect is to render fire an important tool for selectively altering the relative abundance of target species over long time spans.

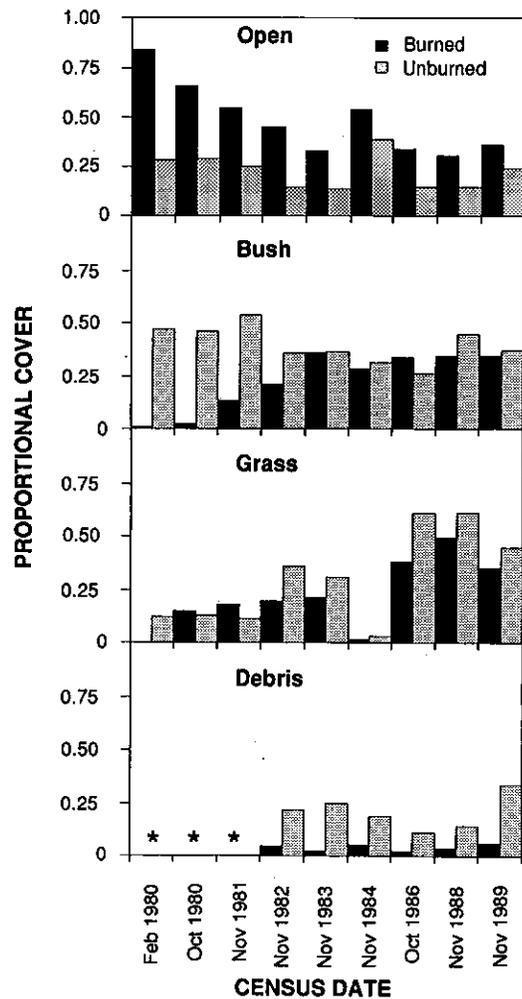


Figure 5. Total number of individuals of four common rodent species recorded on burned and unburned halves of the Motte Rimrock Reserve study grid during 12 standard 3-night censuses. D.a. = *Dipodomys agilis*; C.f. = *Chaetodipus fallax*; P.m. = *Peromyscus maniculatus*; P.e. = *Peromyscus eremicus*.

Indeed, our examples show that it often will be possible to predict *a priori* how a given small mammal species will respond to fire, from a knowledge of the species' habitat affinities and other aspects of its natural history. This prediction is at least qualitatively accurate, and can even be quantitative in terms of the relative abundances of different species in a community (Price and Waser 1984). In either case, the value of the prediction is far from trivial. It presents us with the possibility of designing fire management strategies for native habitats that will achieve defined goals in terms of small mammal populations, without the need for a long series of experimental trials beforehand.

If multispecies conservation is a primary goal, then prescribed fires may best be applied in a mosaic fashion to enhance habitat heterogeneity and maintain species with diverse habitat affinities in the region. The mosaic patches need not necessarily be large to be effective for small mammals: our Lake Perris study shows that populations of Stephens' kangaroo rat respond rapidly to fire-induced habitat alterations less than one hectare in area. In fact, patchiness on a relatively small spatial scale facilitates recolonization because immigration sources are nearby. The importance of this scale effect is that even relatively small fragments of native habitat might be managed successfully with a variety of fire treatments to maintain a high diversity of species of small mammals and other organisms.

A mosaic burning strategy also would help to prevent a catastrophic, large-scale fire that would convert large areas to a single habitat type. At the same time, it should be recognized that the long-term response of vegetation to fire may not conform to a successional model, but rather to essentially irreversible changes in species composition and structure (the state transitions of Westoby et al. 1989). Thus, great care must be taken in fire management to avoid undesirable transitions, the obvious example being the conversion of shrubland to grassland that has occurred so frequently in California (d'Antonio and Vitousek 1992).

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