SURVIVAL AND ABUNDANCE OF THREE SPECIES OF MICE IN RELATION TO DENSITY OF SHRUBS AND PRESCRIBED FIRE IN UNDERSTORY OF AN OAK WOODLAND IN CALIFORNIA

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ABSTRACT—We investigated effects of prescribed understory fire and shrub density on the pinyon deermouse (*Peromyscus truei*), brush deermouse (*P. boylii*), and California pocket mouse (*Chaetodipus californicus*) in a mixed blue oak-coast live oak (*Quercus douglasii-Q. agrifolia*) woodland of coastal-central California. We simultaneously estimated survival and abundance of all species during pre-burn and post-burn. Abundance of pinyon deermice and California pocket mice was significantly higher in plots with high (>25%) shrub cover compared to plots with low (<10%) shrub cover. A light-to-moderate intensity, prescribed, understory fire had no significant effect on survival for any of the three species we investigated. The fire significantly reduced abundance of pinyon deermice in the trapping session immediately after the fire, but abundance increased in subsequent trapping sessions relative to controls. Low intensity, prescribed, understory fire in oak woodland is unlikely to significantly alter populations of rodents if patches of well-structured habitat are maintained. Benefits of prescribed fire for oak woodlands in reduction of the risk of wildfire and rejuvenation of vegetation likely outweigh any short-term negative effects on populations of mice.

RESUMEN—Investigamos el efecto de la quema prescrita del sotobosque y la densidad de los matorrales en el ratón de campo (*Peromyscus truei*), el ratón arbustero (*P. boylii*) y el ratón de bolsillo (*Chaetodipus californicus*) en un bosque mixto de robles (*Quercus douglasii-Q. agrifolia*) de la zona costera central de California. Hicimos cálculos simultáneos de la supervivencia y abundancia de todas las especies antes y después de la quema. La abundancia de los ratones de campo y de bolsillo fue significativamente mayor en parcelas con un nivel alto de cobertura de arbustos (>25%) en comparación a parcelas con un nivel bajo de cobertura de arbustos (<10%). Una quema prescrita de intensidad ligera a moderada del sotobosque no tuvo efectos significativos en la supervivencia de las tres especies bajo investigación. El fuego redujo marcadamente la abundancia de ratones de campo en la sesión de captura inmediatamente después del incendio, pero en relación a la población control, la abundancia aumentó en sesiones de captura subsecuentes. La quema prescrita de baja intensidad del sotobosque en un bosque de robles tiene pocas probabilidades de cambiar significativamente la población de roedores si se mantienen parches de hábitat bien estructurados. Los beneficios que la quema prescrita en bosques de robles tiene en la reducción de vegetación combustible y el rejuvenecimiento de la vegetación probablemente son mayores que cualquier efecto negativo a corto plazo en las poblaciones de ratones.

Small mammals serve ecologically important functions in woodland ecosystems, serving as omnivorous predators and prey, dispersers of seed, soil fungi, and nitrogen-fixing bacteria, and as soil conditioners (Brown and Harney, 1993; Hallett et al., 2003). In oak (*Quercus*) woodlands of western North America, healthy populations of small mammals are a key food source for mesocarnivores, raptors, and federally listed or state-listed species, e.g., the California spotted owl (*Strix occidentalis occidentalis*; Verner et al.,

1992). Recurrent fire always has been an important feature in oak-woodland ecosystems (Johnston, 1970; Lewis, 1973) and has been an important factor in the evolution of species occurring there. Prescribed fire for management of vegetation is common in western oak woodlands, but data on response of small mammals to fire, especially mortality information, are rare. Jones (1992) reviewed effects of fire on *Peromyscus* in various habitats throughout the United States, but she found no study in western oak

woodland and none on our *Peromyscus* of interest, i.e., brush deermouse (*P. boylii*) and pinyon deermouse (*P. truei*). Jones (1992) did not review the California pocket mouse (*Chaetodipus californicus*) in oak woodland. Studies reviewed by Jones (1992) of other *Peromyscus* in oak or hardwood habitats in woodlands of the midwestern or eastern United States reported that post-fire responses varied depending on duration and intensity of fire, and characteristics of habitat. Abundance of the North American deermouse (*Peromyscus maniculatus*) and white-footed deermouse (*P. leucopus*) increased after a prescribed burn that was characterized as hot and fast in oak savanna of Minnesota (Tester, 1965). The fire killed many scattered shrubs and mature oak trees that dominated the area (northern pin oak *Quercus macrocarpa* and burr oak *Q. ellipsoidalis*). Tester (1965) attributed much of the postfire increase in *Peromyscus* to habitat improvement due primarily to nearly complete removal of litter. Other studies of effects of fire on *Peromyscus* in hardwoods showed both increase and decrease in size of populations (Jones, 1992).

Since the review by Jones (1992), Kirkland et al. (1996) reported that white-footed deermice were nearly twice as abundant in unburned forest as in burned forest in Pennsylvania, but this difference disappeared within 8 months of the burn. Kirkland et al. (1996) attributed the rapid recovery of white-footed deermice to the little-burned tree canopy and rapid regrowth of ground cover. Ford et al. (1999) reported that after a high-intensity prescribed fire in oak stands in North Carolina, the postfire abundance of deermice increased relative to the prefire abundance. Finally, in the only two studies of effects of fire on pocket mice (*Perognathus* and *Chaetodipus*) that we found, Fox et al. (1986) reported that abundance of *Chaetodipus* was not affected by fire in oak woodland at Santa Margarita, California, and Simons (1991) reported that in the Sonoran Desert, although a light fire did not affect survival of Arizona pocket mice (*Perognathus amplus*), it decreased abundance.

We report the findings from 9 years (1993–2001) of mark-recapture data for pinyon deermice, brush deermice, and California pocket mice in mixed blue oak-coast live oak (*Q. douglasii-Q. agrifolia*) woodland of the central coast of California. In October 1997, immediately prior to trapping, Cal Fire (California Department of Forestry and Fire Protection, now Cal Fire, in litt.) and the Camp Roberts Fire Department conducted a prescribed, understory fire over 202 ha that included 6 of our 10 1.1-ha study plots. Earlier we reported the impact of the prescribed burn on abundance of selected species of birds, small mammals, amphibians, and reptiles using simple correlation (Vreeland and Tietje, 2002), and for survival and abundance of dusky-footed woodrats (*Neotoma fuscipes*; Lee and Tietje, 2005). Here, for the three species of mice with sufficient captures, we report on abundance and survival in relation to habitat structure and prescribed understory fire in a before-after-control-impact (BACI) design.

MATERIALS AND METHODS—*Study Area*—We conducted this study in oak woodlands of Camp Roberts, a military facility of the California Army National Guard, located in northern San Luis Obispo County, 17 km NW Paso Robles. The facility is 17,800 ha with ca. 7,200 ha classified as oak woodland (Camp Roberts EMAP Phase II, 1989, in litt.). The dominant tree in the study area was blue oak with variable amounts of coast live oak. Understory species included toyon (*Heteromeles arbutifolia*), hollyleaf redberry (*Rhamnus crocea*), bigberry manzanita (*Arctostaphylos glauca*), ceanothus (*Ceanothus*), and poison oak (*Toxicodendron diversilobum*; Vreeland and Tietje 1998). Climate is Mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation averages 38 cm (66-year range, 10.8–74.1 cm), falling almost exclusively as rain during November–March (United States Weather Bureau, Sacramento, California). Prior to this prescribed fire, fire had been excluded from the study area for >15 years (B. Duke, pers. comm.).

Description of Plot—In 1993, we established 10 1.1-ha plots in oak woodland with >50% tree-canopy cover on slopes <20° with north-facing to east-facing aspects and 300–500-m elevation. An eight by eight trapping grid with 15-m spacing was laid out within each plot. Based on vegetation data collected during spring and summer 1995 (Tietje et al., 1997), we characterized the plots as high or low shrub-density (low shrub-density: $n = 4$, mean = 7.4% shrub cover, $SE = 0.4\%$, minimum = 6.8%, maximum = 8.6%; high shrub-density: $n = 6$, mean = 35.6% shrub cover, $SE = 4.0\%$, minimum = 25.5%, maximum = 49.5%). To assess the effect of the prescribed burn on structure of vegetation, we randomly selected 130 sampling points in the treatment area in 1997 before the prescribed burn. Each point formed the center of a 10-m-radius sampling plot. At 10 m from the center of the plot in each of the cardinal directions (N, S, E, W), we measured (1) ground cover by ocularly estimating the percent of a 1-m² frame occupied by green and dried herbaceous vegetation, (2) canopy cover with a convex spherical densiometer (Lemmon, 1956), and (3) vegetational obstruction (an index to shrub cover) by counting the 10-dm sections of a 2.5-m-long vegetation pole (Griffith and Youtie, 1988) that were >25%

covered by vegetation. Within the 10-m-radius circle, we recorded all pieces of large wood ≥1 m long and ≥10 cm diameter at the small end, snags that were ≥10 cm dbh and ≥1.5 m tall, and dwellings of dusky-footed woodrats. We repeated this method on the same plots after the prescribed burn during October–December, and evaluated changes with paired sample *t*-tests (Zar, 1999). Differences were considered significant at $\alpha = 0.05$.

Fire—Immediately prior to trapping in October 1997, Cal Fire, in cooperation with the Camp Roberts Fire Department, burned 202 ha of Camp Roberts oak woodland. The burning accommodated our request for an experimental burn for our study area and the Cal Fire fuels-reduction strategy for Camp Roberts. Because of the use of existing dirt-base roads to help contain the fire, the decision on what areas would be burned was not completely under our control, resulting in uneven sample sizes (n = number of plots in a given treatment category). The burned area included one of our low shrub-density study plots and five of our high shrub-density plots. Three plots in the low shrub-density category and one plot in the high shrub-density category remained unburned and served as control plots. Because $n = 1$ in one-half of our four treatment categories, we could not statistically assess shrub-density and fire interactions.

Trapping—We trapped small mammals twice yearly during October 1993 through October 2001, with trapping sessions in May and October. We trapped for 5 consecutive nights each session during 1993–1997 and 3 consecutive nights during 1998–2001 using a single Sherman (H. B. Sherman Traps, Inc., Tallahassee, Florida) live trap (7.6 by 9.5 by 30.5 cm) at each of the 64 stations/plot. Traps were baited with rolled corn, oats, and barley laced with molasses. All captured animals were ear-tagged for individual identification and species, gender, and trap station were recorded, after which the animals were released at site of capture. After May 1995, we also recorded age (adult or juvenile) based on pelage characteristics (>25% gray = juvenile). The University of California, Berkeley, Animal Care and Use Administrative Advisory Committee approved all procedures.

Abundance—We estimated abundance on each 1.1-ha plot using minimum number of animals alive (MNA). We tested effects of shrub-density and fire on abundance using a general-linear model (GLM) using plot as a categorical variable and coding dummy variables for fire and shrub-density factors. We log transformed the response variable MNA (Zar, 1999), and then Cochrane-Orcutt transformed to remove serial autocorrelation (Cochrane and Orcutt, 1949). Diagnostic tests indicated no violation of assumptions for GLM. Factors we included were time (trapping occasion), shrub-density, fire (effect of fire on abundance in the trapping session immediately following the fire), and fireX (the sustained effect of fire on abundance in all trapping sessions after the fire). All effects were considered significant at $\alpha = 0.05$.

For the two species of *Peromyscus*, we computed the ratio of juveniles to adult females in each trapping session from autumn 1995 to autumn 2001 as an indicator of reproductive success. Because we captured only a few juveniles on individual plots, we pooled data from all plots. Therefore, the ratio has no variance statistic. Data from California pocket mice were insufficient to calculate this ratio.

Selection of Survival Models—We used capture-recapture data from October 1993 through October 2001, providing eight trapping sessions before, and nine sessions after the fire treatment. We assigned animals to one of four groups based on the combination of two shrub-density factors (high and low) and two fire factors (burned and control). During selection of the model, we first examined survival and recapture in relation to 10 a priori models of seasonal and annual variation and shrub-density habitat effects. Once the most-parsimonious model of seasonal and annual variation and shrub-density effects for survival and recapture was determined, we examined effects of fire on survival. Effects of fire were added to the best survival model as fire (effect of fire on survival in the interval containing the fire, specifically, the interval from spring 1997 through fall 1997), fireX (sustained effect of fire on survival in all intervals after the fire), and the additive combination of these two effects of fire.

We conducted model selection in program MARK v.3.1 (White and Burnham, 1999). Data were pooled from each trapping session of 3–5 consecutive days; time interval between sessions was 6 months. Probability of recapture (p_i) was estimated for each trapping session (except the first), and probability of local apparent survival (ϕ) was estimated for each interval between trapping sessions. In the recapture-only model type we used, ϕ is the product of true survival and permanent emigration from the trapping area. We followed approaches suggested by Burnham and Anderson (1998) and Lebreton et al. (1992), using Akaike's Information Criterion adjusted for small samples (AIC_c) as the metric of parsimony for the model. We assessed goodness-of-fit for the most general model (group by year by season) by the bootstrapping method ($n = 100$). We accepted a general model if its deviance ranked <90 out of the 100 rank-ordered deviances simulated. For each dataset, we computed the variance inflation factor ($\hat{c}$) to estimate the quasi-likelihood AICc-values ($qAIC_c$). These $qAIC_c$-values were then used to estimate $\Delta QAIC_c$ (qAICc for a given model-$qAIC_c$ for the model with minimum $qAIC_c$). The model with the minimum $qAIC_c$-value and a $\Delta qAIC_c$-value of zero was considered the most-parsimonious model.

During selection of models, we first examined survival and recapture in relation to 10 a priori models of temporal variation and shrub-density habitat effects. In addition to the group-by-year-by-season global model, we considered all additive and interactive models with year, season, and shrub density as variables.

Recapture was modeled in the 10 reduced forms first, holding survival (ϕ) in the global group-by-year-by-season parameterization. Using the most-parsimonious form of recapture, survival was modeled in the 10 reduced forms while holding recapture (p) in its most-parsimonious form. Once the most-parsimonious form of survival and recapture were modeled, effects of fire (fire, fireX, and fire + fireX) were added to the best survival model and ranked. Treatment effects (i.e.,
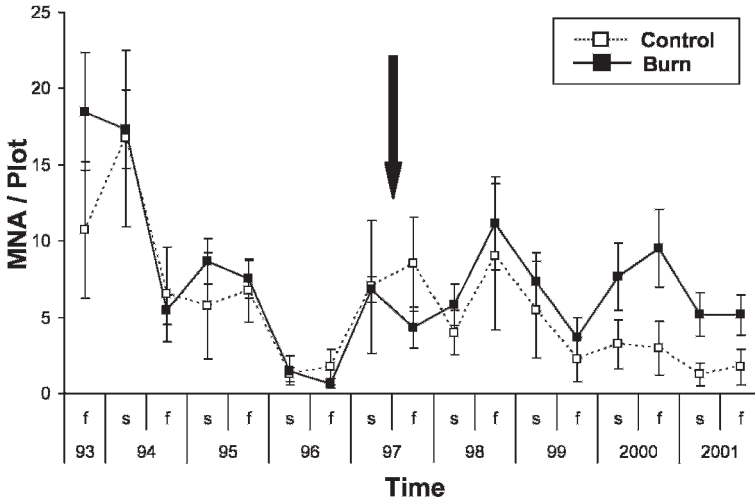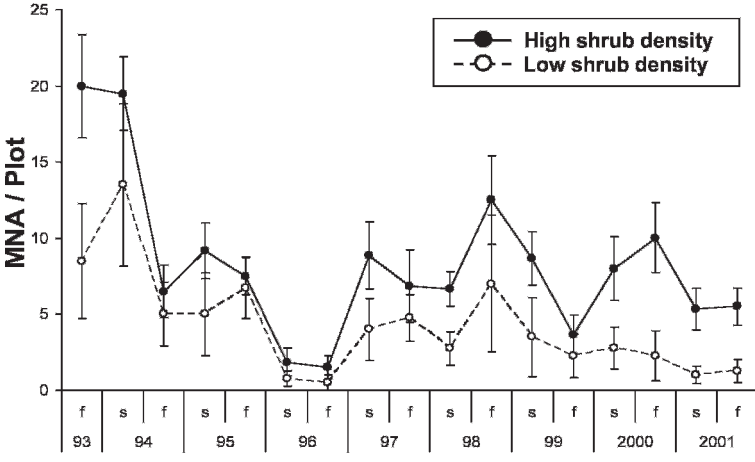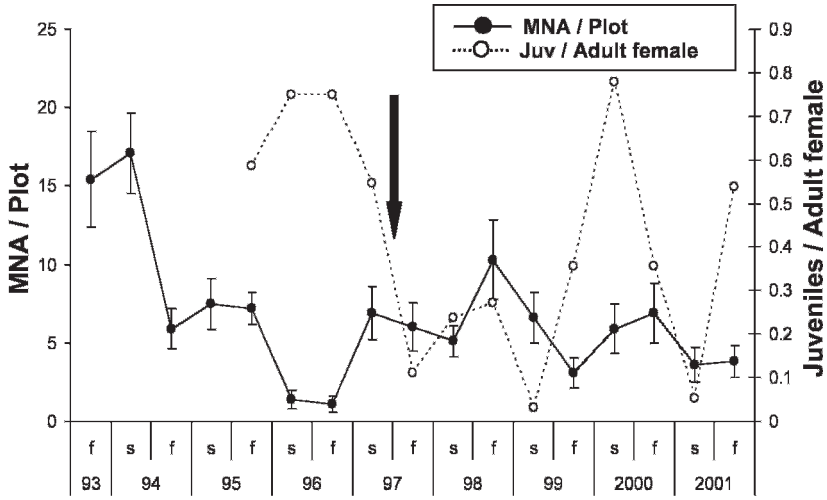
shrub-density and fire) were assessed by examining the rank of the model containing the effect, the model's $\Delta QAIC_c$, and Akaike weights (w_c; Burnham and Anderson, 1998).

Correlations—We used simple correlation coefficients to examine general relationships for survival and abundance among species and between survival and abundance within species, specifying $\alpha = 0.05$ to assess statistical significance.

RESULTS—*Prescribed Fire*—Cal Fire rated the prescribed fire as light to moderate in intensity (3–4 on a 10-point scale). Height of flame generally was <1 m except in a few areas of decadent grasses, chaparral, or accumulations of large wood. Only a few mature trees were killed by the fire. The fire was patchily distributed and carried better through stands of blue oak with abundant grass cover than through stands of mixed oak with thick leaf litter and dense canopy cover. Mineral soil was mostly unexposed except in small areas with high fuel load (dense large wood, chaparral). Area burned on 1-ha plots averaged 46% (range, 30–66%; Vreeland and Tietje 1998).

Significant ($P < 0.05$) vegetational changes before versus after the prescribed burn were detected for herbaceous vegetation (32% before versus 10% after; 70% reduction), understory obstruction (an index to shrub cover; 71% before versus 66% after; 7% reduction), large wood (237 pieces before versus 153 after; 35% reduction), and number of woodrat dwellings (79 woodrat dwellings before versus 56 after; 29% reduction). Much of the reduction in understory obstruction, however, resulted from reduction of herbaceous cover in the lower 0.5 m of the vertical strata of vegetation. Excluding this reduction in herbaceous cover probably would result in no statistical reduction in understory-shrub obstruction. Herbaceous vegetational cover returned to pre-fire cover (i.e., 32%) by 1 growing season after the fire. Vreeland and Tietje (1998) reported additional vegetational responses to the prescribed fire.

Trapping data—We trapped 2,667 individuals: 916 pinyon deermice, 903 brush deermice, and 848 California pocket mice. We detected some evidence of loss of ear tags (i.e., torn ears) for California pocket mice. Whatever loss of ear tags occurred was confused with mortality in data for the pocket mouse, leading to conservative estimates of survival (i.e., lower than true probabilities of survival). Preliminary modeling of probabilities of capture and recapture suggested no difference in trap success, survival, or abundance between trapping sessions.

Abundance of Small Mammals—Abundance (MNA/1.1-ha plot) of pinyon deermice varied among years with no detectable seasonal pattern (Fig. 1, top). The ratio of juveniles:adult females exhibited large variation through time (mean = 0.413; $SD = 0.266$), with productivity peaking and crashing every 18–24 months (Fig. 1, top). After controlling for temporal variation and effects of fire, abundance of pinyon deermice was significantly greater in high shrub-density plots versus low shrub-density plots ($t = 4.067$; $P < 0.001$; Fig. 1, middle). After controlling for temporal variation and shrub density, abundance of pinyon deermice was significantly lower on burned plots compared to unburned plots in the trapping session immediately after the prescribed fire ($t = 3.082$; $P = 0.002$; Fig. 1, bottom). However, by the trapping session in spring following the fire and in each subsequent trapping session to the end of the study, abundance was higher on burned plots. Pinyon deermice exhibited a strong trend ($t = 1.923$; $P = 0.056$; Fig. 1, bottom) toward higher abundance on burned plots.

Abundance (MNA/1.1-ha plot) of brush deermice varied through time with no detectable seasonal pattern (Fig. 2, top). The ratio of juveniles:adult female exhibited large variation through time (mean = 0.244; $SD = 0.223$), with clear peaks in productivity every 18 months (Fig. 2, top). After controlling for temporal variation and effects of fire, abundance of brush

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FIG. 1—Abundance (mean ± *SE*) of pinyon deermice (*Peromyscus truei*) as minimum number of animals/1.1-ha plot (MNA/Plot) in autumn and spring 1993–2001 on 10 plots at Camp Roberts, San Luis Obispo Co., California. Top graph shows total abundance, as well as number of juveniles/adult female. Middle graph shows abundance on high (>25%) and low (<10%) shrub-density plots. The effect of shrub density is significant ($P < 0.05$) in all time periods (i.e., the 17 trapping sessions). Bottom graph shows abundance on plots burned immediately prior to the trapping session in autumn 1997 relative to control plots. The post-fire effect is significant ($P < 0.05$) in all periods after the fire (i.e., spring 1998 to autumn 2001 trapping sessions). Arrow indicates time of prescribed burn.
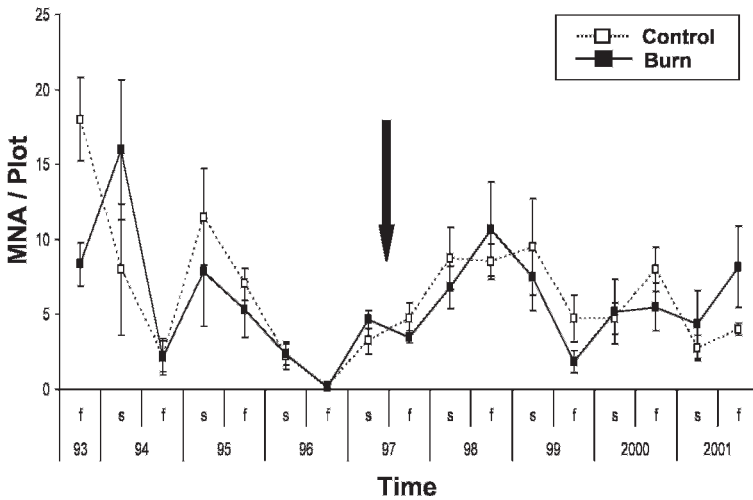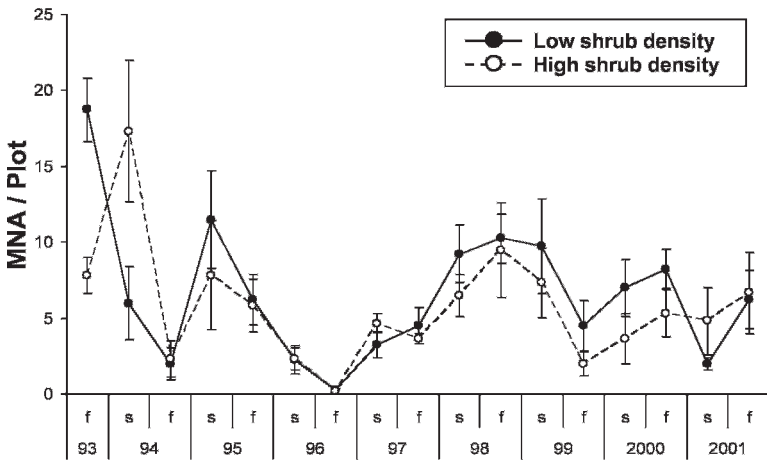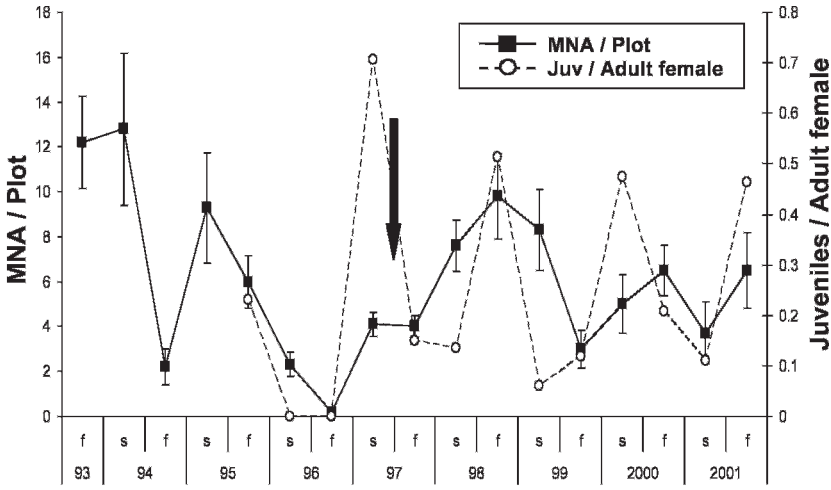
deermice was not significantly different between high and low shrub-density plots ($t = -1.018$; $P = 0.310$; Fig. 2, middle). After controlling for temporal variation and shrub density, abundance of brush deermice was not significantly affected in the trapping session immediately after the prescribed fire ($t = -0.777$; $P = 0.438$) or in all subsequent trapping sessions relative to control plots ($t = -0.566$; $P = 0.572$; Fig. 2, bottom).

Abundance (MNA/1.1-ha plot) of California pocket mice varied through time with a significant seasonal difference ($t = 13.400$; $P < 0.001$); populations in autumn averaged 3.2 times greater than spring (Fig. 3, top). After controlling for temporal variation and effects of fire, abundance of California pocket mice was significantly greater in high shrub-density plots than in low shrub-density plots ($t = 1.997$; $P = 0.048$), but the treatment (shrub density) effect of size (Zar, 1999) was small (Fig. 3, middle). After controlling for temporal variation and shrub density, abundance of California pocket mice was not significantly affected on treatment grids in the trapping session immediately after the prescribed fire ($t = 0.806$; $P = 0.421$) or in all subsequent trapping sessions relative to control plots ($t = -1.598$; $P = 0.112$; Fig. 3, bottom).

Recapture and Survival—Data for all three species passed goodness-of-fit criteria (deviance rank <90 out of 100 rank-ordered simulated deviances), but we applied variance-inflation factors as a measure of conservatism. Variance-inflation factors were >1.0 for all species (1.020, 1.229, and 1.833 for pinyon deermice, brush deermice, and California pocket mice, respectively; Table 1), indicating slight overdispersion, but they were all <2, indicating the model fit the data adequately.

Probability of recapture of pinyon deermice was most-parsimoniously modeled as a function of shrub density (Table 1), with rates of recapture greater in high shrub-density plots (p intercept = 0.563; high shrub-density $\beta = 1.08$; $SE = 0.507$). Survival of pinyon deermice was

most-parsimoniously modeled by annual variation alone ($\phi[year]$). Survival was slightly less during the interval that included the prescribed fire (Fig. 4, top), albeit not significantly (fire $\beta = -0.656$; $SE = 0.565$).

Probability of recapture of brush deermice was most-parsimoniously modeled as a constant. Survival was most-parsimoniously modeled with annual variation ($\phi[year]$), with some evidence for higher survival in high shrub-density plots (high shrub-density $\beta = 0.197$; $SE = 0.210$; Fig. 4, middle). Survival was slightly reduced in the interval that included the prescribed fire, but not significantly (fire $\beta = -0.493$; $SE = 0.956$).

Probability of recapture of California pocket mice was most-parsimoniously modeled with seasonal differences. Probability of survival of California pocket mice was most-parsimoniously modeled with a shrub-density effect, with higher survival in high shrub-density plots (Fig. 4, bottom). Survival was slightly elevated in the interval that included the prescribed fire, and remained slightly higher in all intervals following the fire (Fig. 4, bottom), but neither effect was significant (fire $\beta = 0.596$; $SE = 0.910$; fireX $\beta = 0.203$; $SE = 0.509$).

Correlations—Probability of survival and abundance were positively correlated among species, significantly so between the two species of *Peromyscus* (ϕ $r = 0.84$, MNA $r = 0.89$, $P < 0.001$). This relationship was weaker between brush deermice and California pocket mice (ϕ $r = 0.57$, $P = 0.020$; MNA $r = 0.31$, $P = 0.230$) and between pinyon deermice and California pocket mice (ϕ $r = 0.40$, $P = 0.127$; MNA $r = 0.44$, $P = 0.077$). Within species, abundance and apparent survival were negatively correlated (pinyon deermouse $r = -0.03$, $P = -0.914$; brush deermouse $r = -0.39$, $P = 0.138$; California pocket mouse $r = -0.48$, $P = 0.059$), suggesting some density-dependent effects on survival.

DISCUSSION—This study provides evidence that there can be a short-term depression of abundance and survival of *Peromyscus* after even a low

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FIG. 2—Abundance (mean $\pm$ SE) of brush deermice (*Peromyscus boylii*) as minimum number of animals/1.1-ha plot (MNA/Plot) in autumn and spring 1993–2001 on 10 plots at Camp Roberts, San Luis Obispo Co., California. Top graph shows total abundance, as well as number of juveniles/adult female. Middle graph shows abundance on high (>25%) and low (<10%) shrub-density plots. Bottom graph shows abundance on plots burned immediately prior to trapping session in autumn 1997 relative to control plots. Arrow indicates time of prescribed burn.
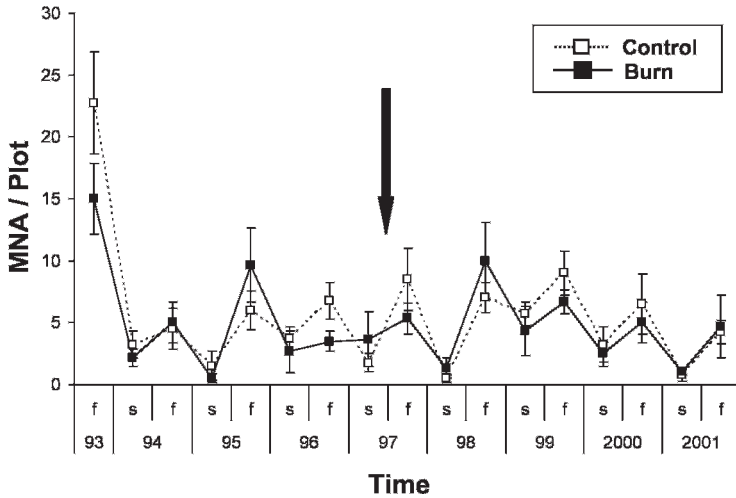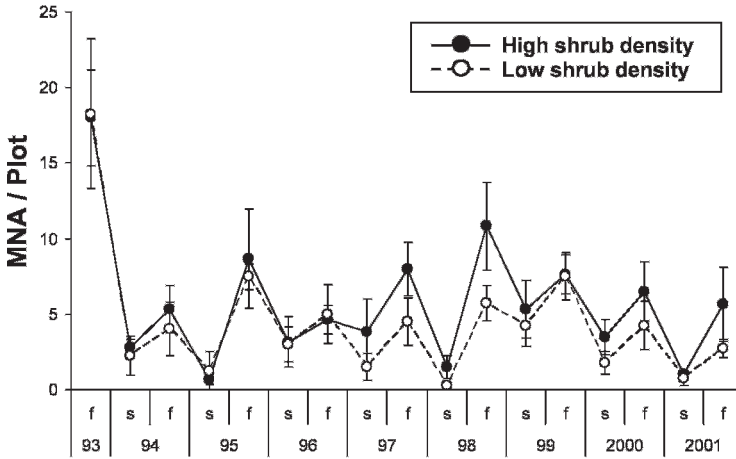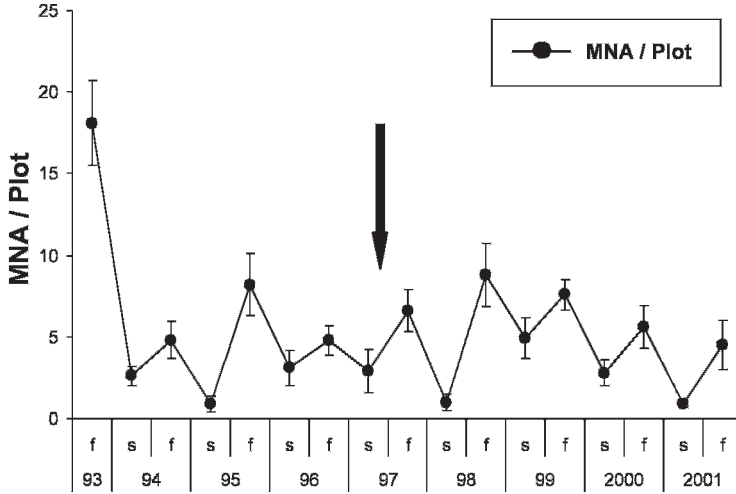
TABLE 1—Highest-ranking models from a priori model set assessing effects of shrub density and prescribed fire on survival and recapture of pinyon deermice (*Peromyscus truei*), brush deermice (*Peromyscus boylii*), and California pocket mice (*Chaetodipus californicus*), Camp Roberts, San Luis Obispo Co., California, 1993–2001. Models are in rank order for each species, the most-parsimonious models at the top (ΔqAICc = 0). QAICc weight gives strength of evidence for a given model as the best in the set. Notation of model: ϕ = apparent survival, p = recapture probability, $\hat{c}$ = variance inflection factor, k = number of parameters, shrub = a difference according to shrub-density group (high or low), fire = a difference on burned plots during the interval when the fire occurred, fireX = a difference on burned plots in all intervals following the fire (long-term alteration of habitat), year = winter year, season = differed between summer and winter, (.) = constant.

Model					
Survival	Recapture	ΔqAIC$_c$	qAIC$_c$ weight	k	Deviance
Pinyon deermouse ($\hat{c}$ = 1.020)					
ϕ (year)	p (shrub)	0	0.28	10	156.5
ϕ (year + fire)	p (shrub)	0.67	0.20	11	155.1
ϕ (year + season)	p (shrub)	1.21	0.16	11	155.7
ϕ (year + fireX)	p (shrub)	1.85	0.11	11	156.3
ϕ (year + shrub)	p (shrub)	2.00	0.11	11	156.4
ϕ (year + fire + fireX)	p (shrub)	2.71	0.07	12	155.1
ϕ (year + season + shrub)	p (shrub)	3.19	0.06	12	155.6
ϕ (year $\times$ season)	p (shrub)	8.26	0.00	17	150.4
Brush deermouse ($\hat{c}$ = 1.229)					
ϕ (year)	p (.)	0	0.29	9	130.9
ϕ (year + shrub)	p (.)	1.16	0.16	10	130.1
ϕ (year + fire)	p (.)	1.78	0.12	10	130.7
ϕ (year + season)	p (.)	2.04	0.10	10	130.9
ϕ (.)	p (.)	2.16	0.10	2	147.3
ϕ (year + season + shrub)	p (.)	3.20	0.06	11	130.1
ϕ (shrub)	p (.)	3.59	0.05	3	146.7
ϕ (season)	p (.)	3.80	0.04	3	146.9
California pocket mouse ($\hat{c}$ = 1.833)					
ϕ (shrub)	p (season)	0	0.24	4	45.4
ϕ (.)	p (season)	0.34	0.20	3	47.8
ϕ (shrub + fire)	p (season)	1.64	0.11	5	45.1
ϕ (season + shrub)	p (season)	1.79	0.10	5	45.2
ϕ (shrub + fireX)	p (season)	1.87	0.09	5	45.3
ϕ (season)	p (season)	2.13	0.08	4	47.6
ϕ (year)	p (season)	3.22	0.05	10	36.4

intensity, understory prescribed burn. Number of pinyon deermice was significantly reduced on burned plots in the interval containing the fire (i.e., the interval from spring 1997 through autumn 1997). Although we did not detect a similarly large change in abundance of *Peromyscus boylii* after the fire, survival estimates of both species of *Peromyscus* were marginally lower, with survival of the pinyon deermouse reduced more than survival of the brush deermouse. This difference can be attributed to the affinity of the pinyon deermouse for more flammable chaparral habitats (McCabe and Blanchard, 1950), or perhaps because of the more arboreal nature of brush deermice (Holbrook, 1979) that enabled them to escape.

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FIG. 3—Abundance (mean ± *SE*) of California pocket mice (*Chaetodipus californicus*) as minimum number of animals/1.1-ha plot (MNA/Plot) in autumn and spring 1993–2001 on 10 plots at Camp Roberts, San Luis Obispo Co., California. Top graph shows total abundance, middle graph shows abundance on high (>25%) and low (<10%) shrub-density plots, and bottom graph shows abundance on plots burned immediately prior to trapping session in autumn 1997 relative to control plots. Arrow indicates time of prescribed burn.
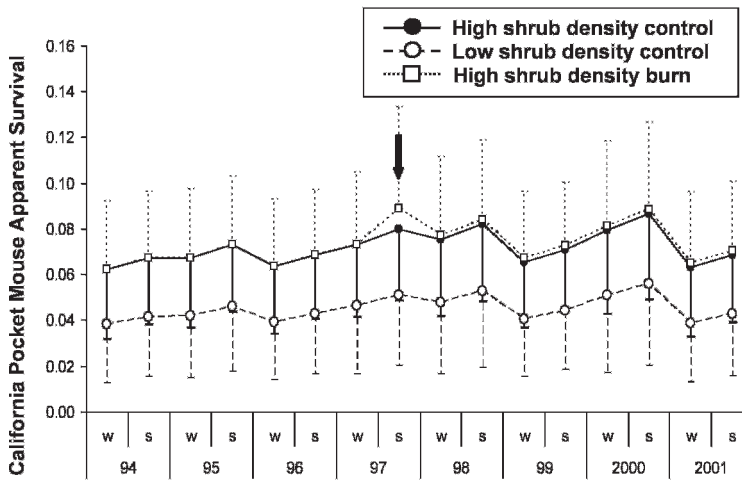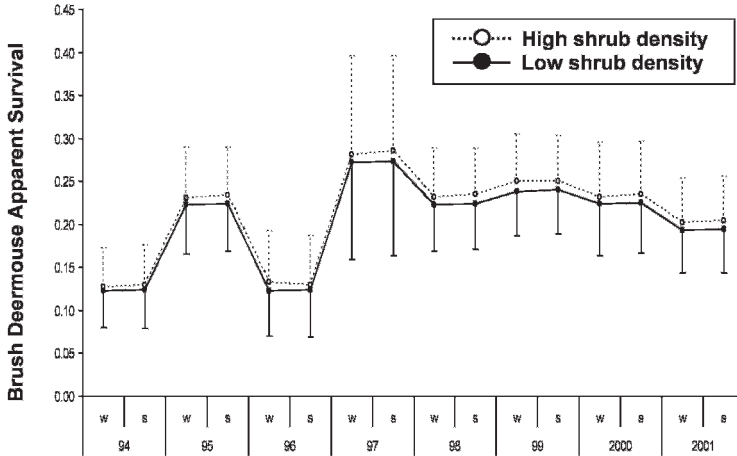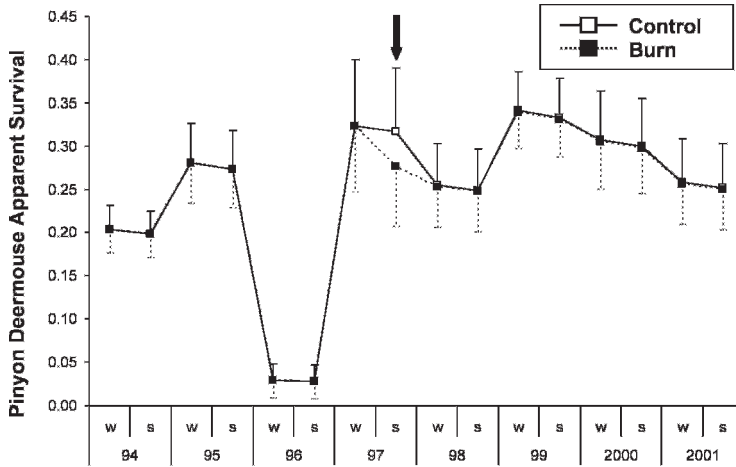
The mostly minimal short-term effects of the fire are not surprising. The oak woodlands in the high country at Camp Roberts consist of a mosaic of microhabitats that differ in susceptibility to fire. Only about one-half of the treatment area burned, and burning was of low intensity and limited to the understory. Those portions of treatment plots with dense shrub understory, where most small mammals were trapped, did not carry the fire and remained unburned. Furthermore, small mammals in western North America evolved with fire and have adaptations to escape adverse effects of fire. The California pocket mouse is the only species of mouse trapped at Camp Roberts that burrows underground (Tinkle and Harmon, 1970), but many extant burrows and other subterranean excavations exist in which the *Peromyscus* could have escaped the fire. Pinyon and brush deermice are scansorial and arboreal (Smart, 1978), and these adaptations provide other means to escape from understory fire. Monimeau et al. (2002), working in the Mediterranean region of Tordères, France, observed similar results for long-tailed field mice (*Apodemus sylvaticus*) in a 4.5-ha patchy burn of low (<2 m), shrubby underbrush. The shrub like kermes oak (*Quercus coccifera*), *Cistus*, and heather (*Erica arborea*) predominated.

The effects on *Peromyscus* were short lived. Abundance of pinyon deermice increased by the following spring, apparently due to the uncovering of food sources by the fire, followed in winter and spring by rejuvenation of vegetation, which improved hiding and reproductive cover, as has been discussed in other studies of small mammals (e.g., Kirkland et al., 1996; Ford et al., 1999). Further, in addition to increased availability of seeds to granivores due to removal of ground cover, Buckner and Landers (1979) reported increased seed production resulting from rapid vegetative regrowth following burns. McGee (1982) attributed rapid population recovery of the North American deermouse (*P. maniculatus*) following fire to the increased

reproductive potential associated with increased availability of food. Abundance of *Peromyscus* is regulated primarily by food supply (Montgomery, 1989). That brush deermice, with a similar diet to pinyon deermice (Jameson, 1952; Holbrook, 1979), did not also show increased survival and abundance in the post-fire environment is perplexing, but might simply reflect increased food sources for the pinyon deermouse after the fire and interspecific resource partitioning.

Results of this study point out the importance of shrubs to populations of mice. Abundances of pinyon deermice and California pocket mice were significantly higher in the high-shrub-density study plots. Our finding that brush deermice were not more abundant in high-shrub density than in low-shrub-density oak woodland at Camp Roberts is consistent with descriptions in Quast (1954) and Fellers (1994) of brush deermice as more common in open habitat. However, in New Mexico, Findley et al. (1975) reported that dense, shrubby vegetation was important to brush deermice, and where more open vegetation types occurred, brush deermice were uncommon. In the Southwest region as a whole, Wilson (1968) noted that brush deermice replaced pinyon deermice where oak or other deciduous shrubs became common. Differences in methods and habitat types between our study and those mentioned make comparisons problematic. Consideration should be given to managing prescribed burns so that patches of shrubs are left intact.

Adler and Wilson (1987) determined that populations of *Peromyscus* in habitats supporting higher abundance also had higher survival, but our findings indicate two possible exceptions. Brush deermice and California pocket mice both had strong negative correlations between survival and abundance. Survival of California pocket mice in high-shrub-density plots was 50% greater than the rate in low-shrub-density plots, but abundance, while significantly different, was more similar between shrub-density types. Dis-

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FIG. 4—Apparent survival (ϕ) of pinyon deermice (*Peromyscus truei*), brush deermice (*Peromyscus boylii*), and California pocket mice (*Chaetodipus californicus*) during winter and summer 1994–2001 at Camp Roberts, San Luis Obispo Co., California. Parameter estimates were model-averaged from all models with qAICc weight >0 from Table 1. Error bars denote 95% confidence intervals of estimates. Arrow indicates time interval (summer 1997) in which the prescribed burn occurred (immediately prior to trapping session in autumn 1997).

persal from high into low-shrub-density plots may have compensated for the higher mortality in low-shrub-density plots. This tentative explanation has the important implication that high-shrub-density oak woodland may function as sources of mice for adjacent, but less well-structured and more-open oak woodland.

Because so many species depend on rodents as prey and for ecosystem services, such as seed dispersal and soil conditioning, it is important to learn about the response of rodents to a needed vegetation-management activity (the prescribed burn). High populations of prey benefit predators (mammalian and avian), which have a much higher resource-management interest than the small mammals that were the focus of our study. The long-term benefits of low-intensity fire to the oak-woodland ecosystem, including reduction of fuels, rejuvenation of vegetation, and creation of habitat mosaics that support greater biodiversity, likely outweigh any short-term (<6-month) negative effects, such as temporary reduction in survival or abundance of mice. This is why the perceived (by the layman) negative effects of controlled burning on wildlife really are not present. Low-intensity burning restores vegetation to a more desirable condition for wildlife and livestock. It is unfortunate that building in wild-land areas, air-pollution concerns, and misunderstanding of prescribed burning by the general public make management by prescribed fire increasingly difficult.

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