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DUSKY-FOOTED WOODRAT DEMOGRAPHY AND PRESCRIBED FIRE IN A CALIFORNIA OAK WOODLAND

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Abstract: We investigated the effects of prescribed understory fire and shrub density on a population of dusky-footed woodrats (*Neotoma fuscipes*) live-trapped each spring and fall from October 1993 to 2001. We performed model selection with program MARK on capture–recapture data using Pollock's robust design to estimate survival and temporary emigration. Abundance increased from 1993 to a peak in 1997 and then decreased steadily from 1997 to 2001, accompanied by reduced reproduction. Survival was age- and time-dependent. Differential temporary emigration probabilities were explained by home-range size differences. Survival and abundance were higher in plots with high shrub cover vs. plots with low shrub cover. A low-medium intensity, prescribed understory fire in the fall of 1997 had no negative effect on survival or temporary emigration. The only fire-related negative demographic effect was a reduction in the number of juveniles per adult female on burned plots in the spring immediately after the fire. Prescribed understory fire in oak woodland is unlikely to alter woodrat populations significantly if patches of well-structured habitat are maintained.

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Dusky-footed woodrats occur in lower elevation forests, woodlands, and chaparral of the Pacific Coast region from Oregon to Baja California, Mexico (Ingles 1995, but see Matocq 2002). Dusky-footed woodrats are the principal food item of spotted owls (*Strix occidentalis*) in the western Sierra Nevada and southern California (Williams et al. 1992). Since the seminal monograph by Linsdale and Tevis (1951), few studies have examined the demography of this species (Smith 1965, Kelly 1989), particularly in relation to prescribed fire and other management practices that alter habitat composition and structure.

Woodlands dominated by oak (*Quercus* spp.) occur over approximately 3 million ha of California (Bolsinger 1988) and include the Northern and Southern Oak Woodland and portions of the Foothill Woodland plant communities as described by Munz (1970). Seventy-five percent of California's oak woodlands are managed for livestock production (Thomas 1997). Such land use can affect woodland understory structure directly by herbivory or indirectly by vegetation management practices to enhance forage production (i.e., prescribed fire). Dusky-footed woodrats have been found to be more abundant in areas of dense shrub cover (Vestal 1938, Linsdale and Tevis 1951, Biswell 1989), but the possible mechanisms behind this differential abundance have not been investigated. Previous studies of the effects of fire on dusky-footed woodrats have largely been confined to coastal sage scrub and chaparral vegetation, and woodrats were more abundant in unburned chaparral habitat relative to burned areas (Lee 1963, Wirtz 1977, Wirtz et al. 1988). Survival and abundance of the white-throated woodrat (*N. albigula*) both decreased in burned vs. unburned areas of Arizona Upland Desert after a 4-ha prescribed fire removed 50–73% of the cover (Simons 1991). Six months after the 16,215-ha Green Meadow Fire in Ventura, California, desert woodrat (*N. lepida*) abundance in burned areas decreased with distance from unburned vegetation edge in coastal sage scrub habitat (Schwilk and Keeley 1998). However, dusky-footed woodrat abundance in burned areas increased with distance from unburned vegetation edge in chaparral habitat (Schwilk and Keeley 1998). Both coastal sage scrub and chaparral habitats are known for fast, hot, stand-replacing fires every 20 to 40 years (Kilgore 1981). In contrast, oak woodlands are characterized by understory fire regimes where most aboveground vegetation survives and only occasional stand-replacing fires occur (Wright and Bailey 1982). The California Department of Forestry and Fire Protection (CDF) Fire Plan 2000 calls for increased use of prescribed fire in oak woodland to manage fuel buildup and live-

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stock forage. The Fire Plan also assumes that prescribed fire is beneficial for wildlife, but data for many species, including dusky-footed woodrats, are not available.

Our objectives were to quantify abundance, survival, temporary emigration, and reproductive success of dusky-footed woodrats in California oak woodlands in relation to understory shrub density and prescribed fire. We also examined reproductive success in relation to prescribed fire, precipitation, food availability, and temperature. Our findings represent 9 years (1993–2001) of mark–recapture data for dusky-footed woodrats in a mixed coast live oak (*Quercus agrifolia*) and blue oak (*Q. douglasii*) woodland of California's central coast.

STUDY AREA

We conducted this study in the oak woodlands of Camp Roberts, a military facility of the California Army National Guard, located in northern San Luis Obispo County. The facility covered 17,800 ha with approximately 7,200 ha classified as oak woodland. The dominant tree was blue oak with variable amounts of coast live oak. Understory shrub species included toyon (*Heteromeles arbutifolia*), redberry (*Rhamnus crocea*), bigberry manzanita (*Arctostaphylos glauca*), ceanothus (*Ceanothus* spp.), and poison oak (*Toxicodendron diversilobum*). Climate was Mediterranean, with cool, wet winters and hot, dry summers. Annual precipitation averaged 38 cm falling almost exclusively as rain between November and March (U.S. Weather Bureau, Sacramento, California, USA).

METHODS

Trapping

In 1993, we established 10 plots in oak woodland with >50% tree canopy cover on slopes <20° with north- to east-facing aspects that were 300–500 m in elevation. Each plot was 1.1 ha and contained an 8-by-8 trapping grid with 15-m spacing. We estimated shrub cover (%) in every plot during spring and summer of 1995 by counting the number of times shrubs were present at 12 points placed systematically around every other trap location (3 points along each of the 4 cardinal directions, spaced 1.7 m apart; Tietje et al. 1997). We defined shrubs as non-*Quercus* spp. woody plants. We divided the 10 plots into 2 categories of shrub density: (1) low shrub density (n = 4, mean = 7.4% shrub cover, SE = 0.4%, range = 6.8–8.6%) and (2) high shrub density (n = 6, mean = 36% shrub cover, SE = 4%, range = 25–50%).

We conducted small-mammal trapping from 1993 through 2001 twice a year during May and October. A single Sherman live trap (7.6 by 9.5 by 30.5 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida, USA) was placed at each of the 64 grid intersections per plot. We trapped for 5 consecutive nights in 1993–1997 and for 3 consecutive nights in 1998–2001. Traps were baited with rolled corn, oats, and barley laced with molasses. Animals were ear-tagged for individual identification (National Band and Tag Co., Newport, Kentucky, USA), and we recorded species, gender, and trap station. We recorded age, based on pelage characteristics (gray = juvenile, brown = adult), after May 1995 (Linsdale and Tevis 1951). Trap mortality was approximately 0.4% of individuals captured and was considered negligible. We only included data for woodrats in this analyses.

Fire

Before 1997, fire had been excluded from the study area for >15 years. Prior to the October 1997 trapping session, the CDF and the Camp Roberts Fire Departments conducted a burn treatment on >200 ha, including 1 of our 4 low shrub density plots and 5 of our 6 high shrub density study plots. The perimeter was burned first, and then the interiors were ignited with drip torches and helicopter-delivered accelerant. Three low shrub density plots and 1 high shrub density plot remained unburned to serve as control plots. Ground, shrub, and canopy cover were measured, and coarse woody debris and woodrat houses were counted on 130 plots in the treatment area <2 months before and <3 months after the fire. We collected data on ground, shrub, and canopy cover using a 1-m^2 frame, shrub pole, and concave densiometer (see Vreeland and Tietje 1998).

Abundance

We estimated abundance of woodrats on each 1.1-ha plot from 1993 through 2001 using minimum number of animals (MNA) captured in the first 3 nights of trapping. We tested effects of shrub density and fire on abundance using a general linear model (GLM) in program NCSS 2000, treating each plot as a subject and using dummy variables to code for effects. We included factors for time, shrub density, control (to control for pre-fire differences in burned vs. control plots), the effect of the fire on abundance in the trapping session immediately after the burn, and the sustained, constant effect of the fire on abundance in all trapping sessions after the burn. The response variable MNA was natural log transformed ($\ln[x + 1]$). Because $n = 1$ in the low shrub density burn and high shrub density control categories, we assumed no interaction of burn and shrub density effects in our GLM analyses. Diagnostic tests indicated no violations of assumptions for GLM.

Reproductive Success

From May 1995 to Oct 2001, we calculated the number of juveniles per adult female woodrat (#juv/af) for each trapping session as an indicator of seasonal reproductive success. The spring #juv/af index was the response variable in a stepwise model selection procedure with 4 environmental predictor variables: (1) precipitation (cm; National Oceanic and Atmospheric Administration [NOAA], Paso Robles, California, USA) in the previous 6 months as a measure of winter/spring vegetation productivity, (2) previous September blue oak mast index, (3) previous September live oak mast index, and (4) minimum temperature (°C) in the previous 6 months as a measure of winter severity (NOAA). Mast indices were the number of acorns counted during 2 15-sec intervals (log-transformed) from a study area in Pozo, California (W. Koenig, University of California, unpublished data).

We tested the effect of the fire on reproduction using a GLM in program NCSS 2000 with spring #juv/af index values as the response variable and dummy variables coding for year, the effect of the fire on #juv/af in the spring immediately after the burn, and the sustained, constant effect of the fire on #juv/af in all spring trapping sessions after the burn. We pooled the 2 shrub density treatments due to low numbers of juveniles captured on individual plots. Diagnostic tests indicated no violations of assumptions for GLM.

Survival and Temporary Emigration

In this analysis, we used capture-recapture data from October 1995 through October 2001, an interval which included 4 trapping sessions before and 9 sessions after the burn treatment when we had determined age of animals at capture. We assigned animals to 1 of 4 groups based on the combination of 2 shrub density factors (high and low) and 2 burn factors (burn and control). We modeled sexes separately due to life history differences (Kelly 1989, Lisdale and Tevis 1951).

We conducted model selection for survival, temporary emigration, capture, and recapture probabilities with program MARK 2.1 (White and Burnham 1999) using Pollock's (1982) robust design model. The robust design model is a combination of the Cormack-Jolly-Seber (CJS) live recapture models (Cormack 1964, Jolly 1965, Seber 1965) and closed capture models. These models are superior to standard (CJS) models, which assume all emigration is permanent, because robust design models include estimators for temporary emigration. The emigration probabilities estimated by the robust design models in this study were strictly temporary; in these models, permanent emigration was confounded with mortality (the complement of survival). Thus, all movement probabilities were estimated only for animals that eventually returned to the trapping grids. Temporary emigration movements off the trapping grids would be primarily associated with animals whose home range was only partially within a trapping grid. The robust design model type is described in detail by Kendall et al. (1995, 1997) and Nichols et al. (1984).

For each trapping session of 3–5 consecutive days, we estimated the probability of first capture (p_{ij}) and the probability of recapture (c_{ij}) (where j indexes the number of trapping occasions within the ith session). For the intervals between trapping sessions, we estimated the probability of survival (S_i), the probability of emigration from the trapping grid area (γ''_i), and the probability of staying away from the trapping grid area given that the animal has left the trapping area (γ'_i).

We followed the approach suggested by Burnham and Anderson (1998) and Lebreton et al. (1992) and selected the model with the lowest Akaike's Information Criterion adjusted for small sample size (AIC_c) as the most parsimonious model for the data set. We assessed fit of the most general model in each data set using the bootstrap approach in program MARK. Although no goodness-of-fit test exists for the robust design model type, we assessed goodness of fit by treating the data as if they were recapture-only data. We ran 100 simulations and compared the resulting deviances with the model deviance from the model ϕ(g*t) p(g*t). There was no evidence for lack of fit, so no variance inflation factors were applied. We used the logit link function throughout these analyses. We used AICc weights as a measure of the strength of evidence for a given model (Mi). AIC_c weight = exp ($-1/2$ * ΔAIC_c of Model Mi) / [sum for all models of exp($-1/2$ ΔAIC_c)] where ΔAIC_c = the difference between the AIC_c for a model and the AICc for the current minimum AIC_c model. For the minimum AIC_c-model, which is the most parsimonious model in the set, the ΔAIC_c is zero. Due to uncertainty inherent in model selection from sample data and because inference should be based on all models in the model set (Burnham and Anderson 2003), we used the multi-model inference procedure of model averaging to obtain parameter estimates used for inference. Model averaging computed a parameter estimate that was the weighted average of the parameter from all models in the candidate set. AIC_c weights were used as the weighting factor.

During model selection, we examined survival and emigration parameters as constants, as linear (A) and quadratic (A^2) functions of age, and with season and year effects including interactions (season * year interactions were denoted as *t* for full time dependence). Emigration was modeled with both emigration parameters equal at a given time step ($\gamma'' = \gamma'$) and with both emigration parameters independent ($\gamma'' \neq \gamma'$). We also tested zero emigration models ($\gamma'' = \gamma' = 0$) (see Kendall et al. 1997). Under robust design, capture and recapture probabilities cannot be modeled as a function of age, but these parameters were modeled as constants and time-dependent. We also tested equality of capture and recapture rates ($p = c$).

To keep the number of parameters manageable, we initially pooled and modeled together all groups for a given sex to determine the most parsimonious time and age structure for the entire sex-specific data set. Next, we divided the same data set into the 4 factor groups and, using the previously determined best age and time structure, we investigated the effects of shrub density and fire. We modeled shrub density as a constant effect through time and as an interaction with time. We modeled fire as a singular event during the summer of 1997 interval and also as a sustained, constant effect in every interval after the summer of 1997.

RESULTS

Fire

The CDF subjectively classified the burn as low to medium intensity. The burn was patchily distributed with an average of 46% (range 30–66%) of each plot in the treatment area classified as burned. Based on vegetation data collected on treatment plots <2 months before and <3 months after the fire, shrub cover was reduced by 7% and grass cover was reduced by 70%. The number of woodrat houses was reduced by 30%, and the number of pieces of coarse woody debris was reduced by 35%.

Abundance

Mean minimum number of animals per plot for all 10 plots (Fig. 1) showed regular seasonal variation: in all years except 1998, more animals were present in spring, the peak breeding period, vs. fall in the same year. There was a generally increasing trend in spring numbers from 1994 to 1997. From 1997 to 2001, the previously evident seasonal variation was severely dampened, and numbers decreased from the study period maximum of 45 ± 8 (mean ± SE) in spring 1997 to the minimum of 10 ± 3 woodrats per plot in fall 2001.

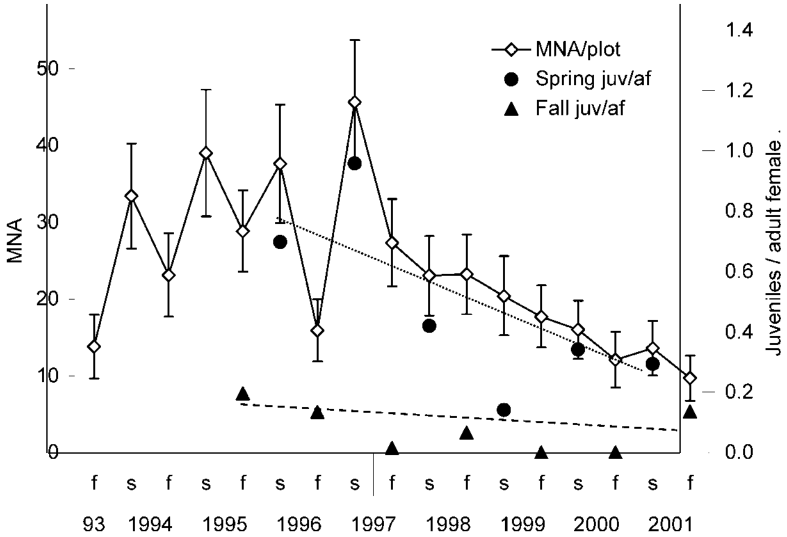

Fig. 1. Dusky-footed woodrat (*Neotoma fuscipes*) abundance, as minimum number of animals (MNA) and number of juveniles per adult female (#juv/af) in spring (s) and fall (f) on 10 plots (1.1ha), 1995–2000, at Camp Roberts, California, USA. MNA is given as mean ± SE for all 10 plots. Dotted line is best fit for spring #juv/af; dashed is best fit for fall #juv/af.

After controlling for temporal variation, differences in woodrat abundance for plots with high- vs. low-density shrub cover were highly significant (β = 1.09, SE = 0.20, *t*

= 5.55, $P < 0.0001$) with high shrub density plots supporting an average of 3 times the numbers of woodrats found on low shrub density plots.

After controlling for the systematic, pre-fire difference in treatment versus control plots, woodrat abundance on plots that were burned did not change significantly in the trapping session immediately after the fire ($\beta = 0.24$, SE = 0.50, $t = 0.49$, $P = 0.63$). There also was no significant sustained change in woodrat abundance ($\beta = 0.18$, SE = 0.23, $t = 0.77$, $P = 0.44$) due to fire-induced habitat alteration.

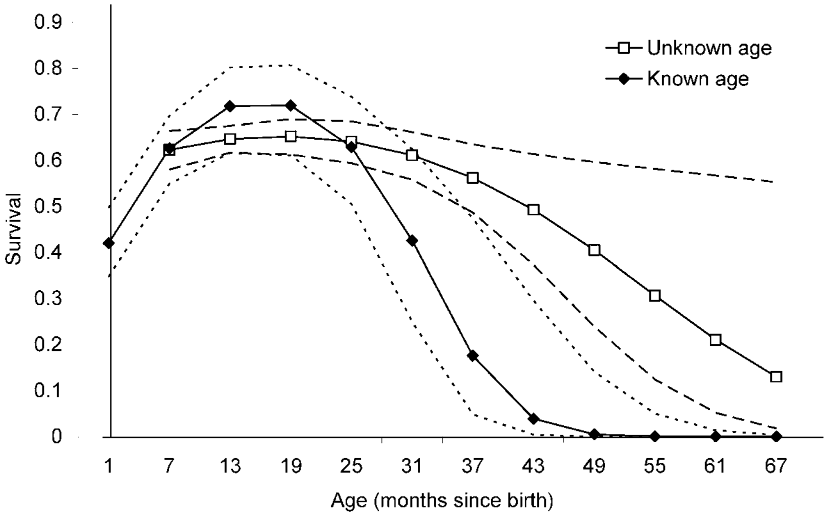

Fig. 2. Survival (S) by age (months since birth) for known (captured as juveniles) and unknown (minimum) age female dusky-footed woodrats (*Neotoma fuscipes*) at Camp Roberts, California, USA, 1995–2000. Survival estimates were calculated from beta coefficients of model {$S(A^2+t)\ \gamma'' = \gamma'$ (A+season) p(t,.) = c(t,.)}. Dashed lines are 95% Confidence Intervals of survival estimates.

Reproductive Success

From 1995 to 2001, the #juv/af on all plots, an indicator of reproductive output, showed a declining trend in spring and fall (Fig. 1). After controlling for year, the number of juveniles per adult female in spring was significantly reduced on burn plots in the season immediately after the fire ($\beta = -0.49$, SE = 0.11, $t = -4.23$, $P = 0.002$). There was no significant sustained change in the number of juveniles per adult female as a result of the fire ($\beta = 0.09$, SE = 0.09, $t = 1.04$, $P = 0.37$). Stepwise regression selected previous winter minimum temperature, an indicator of winter severity, as the only significant predictor of spring number of juveniles per adult female, with a positive relationship between the spring #juv/af and previous winter minimum temperature ($n = 6$, $t = 4.13$, $P = 0.015$, $r^2 = 0.81$).

Survival and Temporary Emigration

The first data set on which we conducted model selection was adult females, excluding all animals captured in juvenile pelage. We began with a general model of full age- and time-dependence, including an interaction between those effects, for survival (S), temporary emigration (γ'') and (γ'), and full time-dependence for capture (p) and recapture (c) probabilities. Age was actually minimum age because animals first captured with adult pelage were of uncertain age. We assumed that many of those initial captures were born in the interval since the last trapping session because reproduction is year-round in coastal California woodrats (Linsdale and Tevis 1951), and female woodrats are philopatric to their natal site (Kelly 1989).

We validated the minimum age ≈ actual age assumption by performing model selection on data from known-age females (only animals first captured in juvenile pelage). The most parsimonious models for known-age females and unknown-age females included quadratic age effects on survival that were not significantly different across the first 3 years of life, beyond which very few animals (<5%) survive (Fig. 2).

The most parsimonious model for all adult females (Table 1) was composed of survival (S_{A^2+t}) as a function of the quadratic age trend plus a season * year interaction. This means that survival by age followed the quadratic curve as in Fig. 2, but each 6-month time step had a unique coefficient of time that varied non-systematically during the study. Temporary emigration (γ'' and γ') was random, meaning both parameters were equal ($\gamma'' = \gamma' = \gamma$) at a given time step. Temporary emigration ($\gamma_{A+season}$) was a function of a linear age trend and an additive seasonal effect, meaning γ was constant by 6-month season (summer or winter), but the seasons differed systematically (summer > winter). Seasonal probabilities

Table 1. Initial model selection results and model selection results in relation to fire and shrub density for all female adult (>6 mo old) woodrats (*Neotoma fuscipes*) at Camp Roberts, California from 1993 to 2001. Model selection performed in program MARK using Pollock's robust design. $\Delta AIC_c = 0$ in most parsimonious model. The most parsimonious model has survival as a quadratic function of age and nonsystematic time variation. Temporary emigration is random ($\gamma'' = \gamma'$), is a linear function of age, and varies systematically by season. Capture and recapture probabilities are equal ($p = c$) and are constant within trapping sessions but vary among trapping sessions.

Survival	Immigration/emigration	Capture/ recapture	ΔAIC_c	AIC_c weight	Model likelihood	# of params
Initial modelling						
$S(A^2 + t)$	γ (A+season)	$p = c(t,.)$	0	0.58	1	56
$S(A^2 + t)$	γ (A^2+season)	$p = c(t,.)$	1.98	0.22	0.37	57
$S(A^2 + t)$	γ (season)	$p = c(t,.)$	2.19	0.19	0.33	55
$S(A^2)$	γ (season)	$p = c(t,.)$	8.76	0.01	0.01	57
Shrub and fire effects						
$S(A^2 + t$ + control + ...)	γ (A + season + control + ...)	$p = c(t,.)$				
burn + shrub density	shrub density		0	0.29	1	63
shrub density	burn + shrub density		0.38	0.24	0.83	63
burn + shrub density	burn + shrub density		1.20	0.16	0.55	64
shrub density	shrub density		1.40	0.14	0.50	62
burn + burnX + shrub density	burn + shrub density		2.77	0.07	0.25	65
burn + shrub density	burn + burnX + shrub density		2.88	0.07	0.24	65
burn + burnX + shrub density	burn + burnX + shrub density		4.39	0.03	0.11	66
burn + burnX + shrub density	burn + burnX		6.69	0.01	0.04	64
burn + burnX	burn + burnX + shrub density		16.90	0	0	55
			18.77	0	0	47
burn + burnX	burn + burnX		18.93	0	0	53

decreased in a linear manner as animal age increased. Capture (*p*) and recapture (*c*) probabilities were equal and constant within a trapping session but varied nonsystematically through time. The most parsimonious model of capture and recapture probabilities did not include a difference between 3- and 5-day trapping schedules.

Next, we divided the same adult female data set into 4 groups of animals based on the characteristics of the plots on which they were trapped (high/low shrub density and burn/control). Using the best model from the previous model selection procedure as a starting point, we tested for differences in survival and temporary emigration due to shrub density, fire, and the interaction between shrub density and fire effects (Table 1). We found that we had to control for a systematic difference in survival and temporary emigration parameters between burn and control plots (control effect) before testing for the fall 1997 burn effect.

Animals in high shrub cover plots had a mean survival (S = 0.673 ± 0.022) that was higher than mean survival of animals in low shrub cover plots (S = 0.574 ± 0.059). The temporal variation in survival was lower in high shrub density plots (SD = 0.107) than in low shrub density plots (SD = 0.288; Fig. 3). The fire had a positive effect on survival and temporary emigration parameters during the interval when the burn occurred, but no significant lasting impact on either parameter.

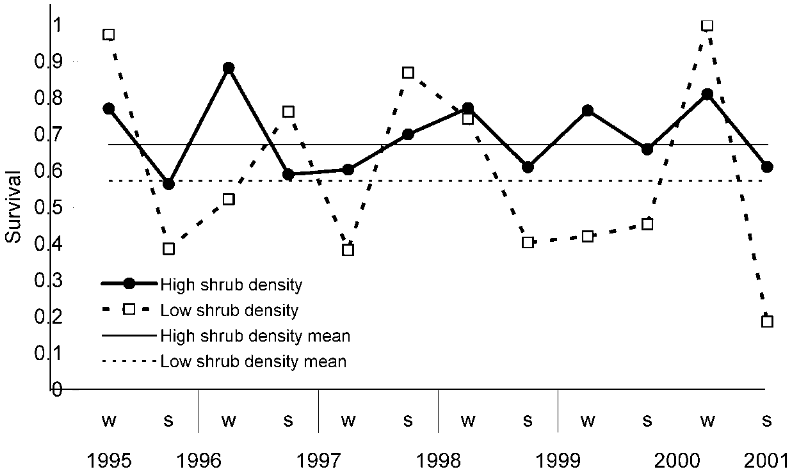

Fig. 3. Annual variation and mean survival over winter (w) and summer (s) for female dusky-footed woodrats (*Neotoma fuscipes*) in high (solid line) and low (dotted line) shrub density plots at Camp Roberts, California, USA, 1995–2000. Survival estimates from model averaging of all models in shrub and fire effects model set.

Table 2. Model selection results for all male adult (>6 month old) woodrats (*Neotoma fuscipes*) at Camp Roberts, California, USA, 1993–2001. Model selection performed in program MARK using Pollock's robust design. $\Delta AIC_c = 0$ in most parsimonious model. The most parsimonious model has survival as a quadratic function of age and nonsystematic time variation. Temporary emigration parameters are independent ($\gamma'' \neq \gamma'$). Probability of leaving the trapping area (γ'') varies nonsystematically by time. Probability of remaining off the trapping area (γ') is a quadratic function of age and varies nonsystematically through time. Capture probability (p) is constant within and among trapping sessions. Recapture probability (c) varies nonsystematically through time within and among trapping sessions.

Survival	Temporary emigration		Capture	Recapture	ΔAIC_c	AIC_c weight	Model likelihood	# of params
$\{\mathrm{S}(\mathrm{A}^2 + t)$	$\gamma''(t)$	$\gamma'(A^2 + t)$	$p(.,.)$	$c(t, t)$	0	0.70	1	73
$\{S(A^2 + t)$	$\gamma''(.)$	$\gamma'(A^2+ t)$	$p(.,.)$	$c(t, t)$	3.16	0.14	0.21	66
$\{S(A^2 + t)$	$\gamma''(\mathrm{A})$	$\gamma'(A^2 + t)$	$p(.,.)$	$c(t, t)$	3.87	0.10	0.14	67
$\{S(A^2 + t)$	$\gamma''(\mathrm{A}^2)$	$\gamma'(A^2 + t)$	$p(.,.)$	$c(t, t)$	5.91	0.04	0.05	68
$\{S(t)$	$\gamma''(.)$	$\gamma'(t)$	$p(.,.)$	$c(t, T)$	9.97	0.00	0.01	76

We also performed model selection on the male data set. We began with all adult males and selected the most parsimonious age and time structure. The most parsimonious model for all males (Table 2) was composed of survival (S_{A^2+t}) as a function of the quadratic age trend plus a season * year interaction that was identical in structure to the female model. Temporary emigration parameters (γ'' and γ') were modeled independently. Probability of leaving the trapping area (γ'') varied nonsystematically by time, while probability of remaining off the trapping area (γ') was a function of a quadratic age trend plus a nonsystematic time coefficient. Male data were insufficient to model the additional combined effects of shrub density and fire.

DISCUSSION

Overall Abundance

On all plots, regardless of shrub density or burn treatment, the abundance of woodrats steadily decreased from fall 1997 to fall 2001, so the effect was widespread at the moderate scale (6 km) represented by our grids. We found there was no decreasing trend in survival estimates for any adult age class through time, so increasing adult mortality or dispersal did not seem to be driving the falling abundance. Oli and Dobson's (1999, 2001) simulation studies showed age at maturity and juvenile survival to potentially be the main demographic drivers of small-mammal population cycles. We did not record reproductive state of individual adult females to track age of first reproduction. Our estimates of survival for independent juveniles did not decline during the study period, but the #juv/af served as a proxy for survival of offspring from conception to independence.

In the springs of 1996 and 1997, the Camp Roberts woodrat population was at its peak, and the #juv/af was also at its highest. During the decrease in abundance from fall 1997 to fall 2001, the #juv/af also decreased. The reduced #juv/af was mirrored in the reduced seasonal variability after 1997 indicating that fewer independent offspring were produced during the main spring breeding season. The decrease in the #juv/af could be due to either a reduction in female fertility or reduced survival of offspring in the interval between birth and independence, beyond which they would have been available for capture. The mechanisms of reduced survival for dependent offspring could be malnutrition, nest predation, parasites, or disease (Batzli 1992). The #juv/af was significantly related only to minimum temperature in the previous winter. Winter and spring vegetation (indexed by precipitation) and mast production were not significant predictors of the spring number of juveniles per adult female. Thus, regardless of food availability, severe winters seem to have reduced the condition of females such that either they produced fewer offspring, or fewer young survived to independence, but those individuals that did reach independence suffered no further reduction in survival. We have no data on the abundance of either predators or parasites during the study period.

Effects of Shrub Density and Prescribed Fire

The population dynamics we reported support the findings of previous studies that dusky-footed woodrat abundance was positively associated with shrub density (Vestal 1938, Linsdale and Tevis 1956, Biswell 1989). We estimated abundance and survival of woodrats simultaneously relative to shrub densities and found that the 2 parameters are both positively correlated with shrub density. Adler and Wilson (1987) found that populations of wood mice (*Peromyscus* spp.) in habitats supporting higher abundance also had higher survival. *Peromyscus* abundance is primarily regulated by food supply (Montgomery 1989). Food may be the factor that drives the positive correlation of abundance and survival of woodrats with shrub density, but other factors such as predation may also be important.

We did not detect significant short-term (6 mo) or longer-term (4 yrs post-fire) negative effects of the patchy understory fire on either abundance or survival of woodrats in mixed coast live-blue oak woodland at Camp Roberts. The increased survival we observed in the interval that included the fire could be explained by reduction of predator/competitor numbers or increased food availability. Neither of these is likely, given that the fire occurred at the end of the interval between trapping sessions, meaning any fire-induced mechanism would have to be fast-acting. Because we anticipated only the possibility of a negative impact on survival during the interval that included the fire, we view the detected survival differences between treatment and control plots in the interval when the fire occurred to be an artifact of sampling not attributable to the burn. We did foresee the potential for either positive or negative impacts on survival in the post-fire intervals as a consequence of beneficial or deleterious fire-induced habitat alteration. However, no significant effect on survival or temporary emigration was detected in the post-fire intervals.

The only negative consequence of the fire we detected was a 1-yr reduction in the spring reproductive success (indexed by #juv/af) of females on burned plots. This reduced reproduction could be due to the reduction in available houses for nest sites because many houses were consumed by the fire and new houses are not readily constructed (Linsdale and Tevis 1951). Also, the fire may have altered habitat in the treatment areas in other ways that reduced survival of offspring between conception and independence without affecting adult survival (i.e., by increasing predation pressure on neonates).

In oak woodland, adult woodrats seem not to suffer any reduction in survival or abundance from understory fire of low to moderate intensity and patchy distribution. In contrast, reductions in survival and abundance have been reported for chaparral-dwelling (Wirtz 1977, Wirtz et al. 1988) and desert-dwelling (Simons 1991) woodrats in hotter, more complete burns. However, oak woodlands do occasionally undergo stand-replacing fires that are known to reduce woodrat numbers (Chew et al. 1959).

Temporary Emigration

Temporary emigration movements off and on to the trapping grids would be primarily associated with animals whose home ranges were only partially within a trapping grid. Adult male emigration rate (γ'') averaged 0.357 ± 0.027 (mean ± SE), and the probability of remaining off the study area (γ') averaged 0.492 ± 0.072 throughout the study. Adult female γ'' and γ' were equal and averaged 0.156 ± 0.023 in winter and 0.468 ± 0.030 in summer. Given these parameter estimates, the compound probability of emigrating in 1 interval and remaining off the trapping grids for a second interval was 0.176 for males and 0.073 for females. Male woodrats have previously been reported as more likely to disperse (Linsdale and Tevis 1951, Kelly 1989) and to have larger home ranges than females (Cranford 1977, Kelly 1989). Because dispersal is generally considered a permanent emigration, we attributed sexual differences in temporary emigration probabilities to sexual differences in home-range size.

By the same reasoning, seasonal differences in female temporary emigration probabilities can be explained by the seasonal differences in home-range sizes of female woodrats. Female home ranges are larger in the winter and smaller in the main breeding season (Cranford 1977). The probability of a female being off the grids during the winter, when home ranges are expanded, was 0.38, and the probability of a female being off the grids during the summer, when home ranges are contracted, was 0.08. Cranford (1977) reasoned that the contraction of female home range during the breeding season was due to the higher plant productivity in that season. Another explanation is that the females stay close to their nests to guard against infanticide (Wolff 1993). Individual home ranges show substantial inter- and intra-sexual overlap (Cranford 1977), and the presence of other lactating females, nonpaternal males, and transient nonbreeders could all pose a threat to unguarded neonates.

Assuming home-range size is the main reason for differences in temporary emigration rates, the linearly decreasing trend in temporary emigration for females of increasing age signifies a shrinking of home-range area as females age. Several explanations could apply: young animals may undertake more exploratory movements, older females may enjoy higher rank in the dominance hierarchy and reside in better quality territories that require fewer foraging movements, or older animals may be unable to defend against encroachment by surrounding animals. Another possibility is that older females might show an increase in nest guarding behavior, investing more in the survival of their offspring than younger females do. Life history theory predicts such a trade off (Fisher 1930, Williams 1957, Stearns 1976). As an older female's survival probability decreases with age, greater investment should be made in her offspring's survival.

MANAGEMENT IMPLICATIONS

Low-intensity prescribed fire in oak woodlands is not likely to have significant impacts on populations of dusky-footed woodrats so long as refugia of thick shrub cover remain unburned. The long-term benefits of prescribed fire to the ecosystem, including reduction of fuels, rejuvenation of vegetation, and creation of habitat mosaics that support greater species diversity, likely outweigh any short-term negative effects such as temporary loss of woodrat houses. However, repeated shrub removal may have more significant effects on woodrat numbers by permanently removing nest sites and protective cover. Maintenance of patches of well-structured habitat (>36% shrub cover in areas with >50% tree canopy cover) on the landscape is important in maintaining adequate numbers of woodrats to support predator populations.

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