



## Factors driving California pocket mice (*Chaetodipus californicus*) population dynamics

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Understanding how demographic parameters respond to climatic variables is essential for predicting species' response to changing environmental conditions. The California pocket mouse (*Chaetodipus californicus*) is an inhabitant of coastal-central California oak (*Quercus* spp.) woodland that is undergoing a rapid anthropogenic transformation while also facing effects of global climate change. We analyzed the population dynamics of the California pocket mouse by applying Pradel's temporal symmetry model to a 10-year (2004 – 2013) capture–mark–recapture data set to estimate survival and recruitment rates and realized population growth rate. The overall monthly apparent survival probability ( $\phi$ ) was  $0.76 \pm 0.01$  SE and was slightly higher in the dry season ( $0.79 \pm 0.02$  SE) than the wet season ( $0.74 \pm 0.01$  SE). Coefficients of variation (CV) of temperature and rainfall (with and without a one-season lag), average seasonal temperature, and regional climatic variation (El Niño index) positively influenced  $\phi$ . Overall monthly recruitment rate ( $f$ ) was  $0.17 \pm 0.01$  SE but varied seasonally;  $f$  was substantially higher during the dry season ( $0.39 \pm 0.04$  SE) than the wet season ( $0.09 \pm 0.02$  SE). Average seasonal temperature, CV of temperature and rainfall (without a one-season lag), and total seasonal rainfall (with a one-season lag) positively influenced recruitment, whereas regional climatic variation (El Niño index), total seasonal rainfall (without a one-season lag), and CV of rainfall (with a one-season lag) had a negative effect on  $f$ . Monthly realized population growth rate ( $\lambda$ ) was  $1.00 \pm 0.02$  SE (or  $0.07 \pm 0.02$  SE annually) for the entire study period, but it varied temporally. Our study provides the first estimates of demographic parameters for the California pocket mouse and tests for the influence of climatic variables on these parameters. Although the California pocket mouse population remained relatively stable during our study (as indicated by  $\lambda = 1.00$ ), changing climate and anthropogenic influences on California oak woodland could adversely influence demographic parameters and population dynamics and might also indicate effects of climate change on its ecologically sensitive habitat.

Key words: capture–mark–recapture analysis, climatic effects, demographic parameters, population dynamics, population growth rate, Pradel's model, recruitment, survival

Knowledge of demographic parameters and factors and processes influencing them is necessary for understanding population dynamics and persistence, and the structure and function of ecological communities (Chesson et al. 2004; Thibault and Brown 2008; Thibault et al. 2010; Nichols et al. 2011; Allington et al. 2013). Because small mammals have short generation times and their field studies are logistically less challenging than those of large mammals, they often are used as model organisms for studies of population and community dynamics,

behavioral ecology, and disease ecology (Fryxell et al. 1998; Ostfeld et al. 1998; Ernest et al. 2008; Krebs 2013; Krebs et al. 2013). Understanding the relationship between population dynamics and environmental factors can hold the key to the long-term viability of small mammal species and for maintenance of ecological niches they occupy.

The hypothesis that abiotic factors are the primary drivers of small mammal population dynamics is well tested and continues to receive considerable empirical support

(Holmgren et al. 2006; Kelt 2011). The influence of abiotic factors on population dynamics is better understood in arid and semiarid environments because these are resource-limited regions with highly variable weather patterns (Kelt 2011; Mason-Romo et al. 2017). Intense rainfall events often lead to pulses of high primary productivity that can cause periodic population outbreaks (Beatley 1969; Lima et al. 1999; Orland and Kelt 2007). While long periods of drought can lead to severe population declines, which can adversely impact population persistence (Dickman et al. 2001; Greenville et al. 2012), climatic impacts on small mammal demography and population dynamics usually are not consistent across species with different life-history traits or habitat requirements (Hernández et al. 2005). Species-specific responses to abiotic factors could reset long-term population trends and, together with biotic interactions, alter structure of small mammal communities (Thibault and Brown 2008). Furthermore, species-specific responses of small mammals can be used as an indicator of climate change-induced alterations of ecological systems.

Semiarid, coastal-central California oak (*Quercus* spp.) woodland is undergoing a rapid anthropogenic transformation

whilst also facing the effects of global climate change. Human activities at the interface of residential development and wildland have resulted in the loss of native shrublands (Syphard et al. 2017). Human-caused ignitions also have dramatically increased frequency and intensity of large wildfires (Keeley and Fotheringham 2001); the area burned in southwestern California is predicted to nearly double by mid-century (Yue et al. 2014). These habitat alterations are exacerbated by environmental changes that are occurring rapidly and are expected to continue (Intergovernmental Panel on Climate Change 2014).

We studied the demography and population dynamics of the California pocket mouse (*Chaetodipus californicus*), a small rodent occurring in the central-coastal range woodland of southern California. It has a relatively narrow distribution that extends along the California coast from San Francisco Bay and the San Joaquin Valley south through Baja California and along the Western Sierra Nevada (Fig. 1). Throughout its distribution, it occupies semiarid shrublands and woodlands that are undergoing some of the most pervasive and rapid anthropogenic and environmental changes globally (Alagona et al. 2013). Since the 1970s, urban sprawl into formerly wildland areas has

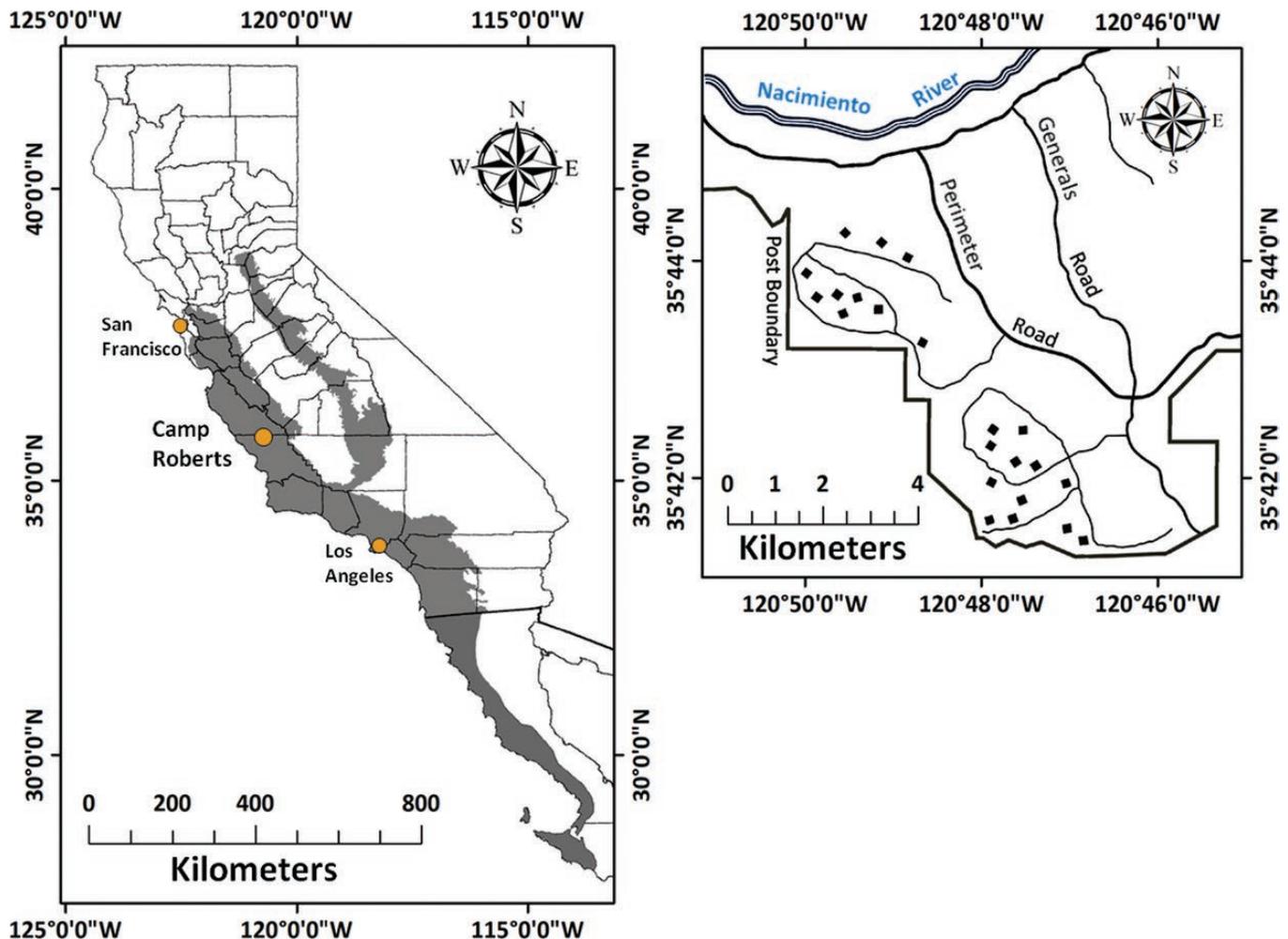


Fig. 1.—Distribution of the California pocket mouse (*Chaetodipus californicus*; gray shading) in California, United States, and Baja California (adapted from Zeiner et al. 1988), and location of the National Guard Post Camp Roberts study site. Inset shows the 22 trapping plots (solid squares) that were sampled in 2004–2013.

proceeded at an ever-accelerating rate. Because the California pocket mouse occupies a narrow area in an ecologically sensitive system that is experiencing diverse, rapid, and widespread alterations, investigating the population dynamics of this little-studied California heteromyid will not only provide essential information about the species but also can serve as an indicator of the climate change-induced alterations of coastal woodlands of central California.

Here, we applied temporal symmetry capture–mark–recapture (CMR) models (Pradel 1996; Williams et al. 2002; Nichols 2016) to a 10-year data set (2004–2013) to (1) provide estimates of apparent survival probability ( $\phi$ ), recruitment rate ( $f$ ), and realized population growth rate ( $\lambda$ ); and (2) investigate the influence of sex, season, and climatic variables (e.g., temperature and rainfall and their variability) on  $\phi$ ,  $f$ , and thus on  $\lambda$ . Given that our study species inhabits a rainfall-limited, semiarid environment, we expected rainfall to positively influence  $\phi$  and  $f$ ; in contrast, we expected that temperature would negatively influence these demographic parameters. Specifically, we predicted that  $\phi$  and  $f$  will be (1) positively influenced by total seasonal rainfall (with and without a one-season lag) via a current season and a delayed increase in plant growth and seed production; (2) negatively influenced by temperature, particularly during the dry season; (3) negatively influenced by variability in temperature and rainfall due to unpredictability in primary production (Huxman et al. 2004); and (4) will be positively affected by El Niño events (a measure of regional climatic variability) due to increased local precipitation.

## MATERIALS AND METHODS

**Study species.**—The California pocket mouse is a nocturnal, mostly solitary, granivore that spends most of the day in its burrow (Tucker 1966). To keep the temperature low and humidity high during the day, pocket mice usually occlude the entrances to their burrows (French 1977). The burrow is used for caches of seeds of forbs and grasses (Tucker 1965), care of neonates, and moderation of microclimate and to reduce vulnerability to predation and wildfires. The California pocket mouse can enter diurnal torpor for up to 24 h (Merritt 1985), an adaptation for energy conservation during periods of food shortage (Tucker 1965). Aboveground activity essentially is restricted to nocturnal foraging and mate finding. From April through July, the one annual litter of about four young (range: 2–7) is produced in the burrow nest (Eisenberg and Isaac 1963).

**Study area.**—We carried out this study at the Camp Roberts National Guard Post (henceforth, Camp Roberts), a 170-km<sup>2</sup> military facility located in coastal central California about midway between San Francisco and Los Angeles (Fig. 1). The climate is Mediterranean. During the 10-year study (2004–2013), the mean monthly rainfall in summer (dry season, May–September) was 2.6 mm (monthly range = 0–37.6 mm). In winter (wet season, October–April), mean monthly rainfall was 52 mm (monthly range = 0–260 mm). The wet season thus accounted for 96% of the annual rainfall. Mean monthly temperature in summer during the 10 years was 12°C (coolest

daily minimum temperature = 2°C and warmest daily maximum temperature = 46°C). Mean monthly temperature during winter was 7°C (coolest daily minimum temperature = –9°C and warmest daily maximum temperature = 41°C). On average, the coldest month was January (mean = 2°C), and the warmest month was July (mean = 12°C) (<https://www.ncdc.noaa.gov/cdo-web/datasets>).

Our study area was located within an 80 km<sup>2</sup> area of open stands of blue oak (*Quercus douglassii*) with a sparse shrub layer of buckbrush (*Ceanothus cuneatus*) and a ground layer of annual grasses (*Avena* and *Bromus* spp.). On the more mesic areas, mixed stands of blue oak and coast live oak (*Q. agrifolia*) predominated with an understory shrub layer of toyon (*Heteromeles arbutifolia*), red berry (*Rhamnus crocea*), coffeeberry (*R. californica*), and manzanita (*Arctostaphylos* spp.). Ground cover included invasive annual grasses, native bunch grasses (*Nassella* spp. and *Festuca* spp.), and forbs such as hummingbird sage (*Salvia spathacea*), wild peony (*Paeonia californica*), and miner's lettuce (*Claytonia perfoliata*). Poison oak (*Toxicodendron diversilobum*) formed dense thickets or grew as a thick vine climbing a tree.

Ecosystem disturbance included fire, grazing, and public recreation. At Camp Roberts, the last wildfire over the study area occurred in 1953 (Fire Chief, Camp Roberts, pers. comm.). The study area is not grazed by livestock and was not used for military training during the study. Public hunting of wild turkey (*Meleagris gallopavo*), quail (*Callipepla californica*), Columbian black-tailed deer (*Odocoileus hemionus columbianus*), and feral pigs (*Sus scrofa*) is allowed on the base.

**Field methods.**—From 2004 to 2013, we trapped rodents in May (spring trapping session) and October (autumn trapping session) for three consecutive nights, resulting in 20 trapping sessions, on twenty-two 8-m × 8-m grids with 15-m spacing between traps (Fig. 1). We placed one Sherman live trap (3 cm × 3.5 cm × 30 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida) within 2 m of each grid intersection. To prevent hypothermia or hyperthermia of animals, we covered traps with leaf litter from the immediate area, and we baited traps with rolled oats, corn, and barley mixed with molasses. At initial capture, we tagged animals in the right ear with a numbered Monel 1005-1L1 tag (National Band and Tag Company, Newport, Kentucky) and recorded tag number, alphanumeric grid location, sex, and age. We did not capture any juveniles (i.e., animals in gray pelage), likely because neonates were not yet born or in the natal burrow during May trapping. We released animals at the location of capture. Because we suspected that tag loss occurred (right ear of some mice was torn, which was indicative of tag loss) during the first 10 years of the longer-term study at Camp Roberts (autumn 1993 to spring 2014; for a detailed description of the longer-term study, see Tietje et al. 2018), we restricted our analysis to data from 2004 to 2013. An experienced field worker (W. D. Tietje, with experience of tagging > 12,000 small mammals) tagged one-third of all small mammals captured from 1993 to 2004 and tagged all captures from 2005 to 2013; torn ears in the animals were not observed during this period, suggesting no evidence of tag loss. Because

Jung et al. (2020) consider 5 years of experience and tagging of > 10,000 animals as “high level of experience,” we are confident that there was almost no tag loss during the 2005–2013 study period. Using our field records, trap mortality was negligible (1.31%). Capture and handling followed the guidelines of the University of California, Berkeley, Institutional Animal Care and Use Committee (University of California, Berkeley Permit R-126A) and guidelines of the American Society of Mammalogists (Sikes et al. 2016).

**Climatic covariates.**—We defined the 5-month period (May–October) between spring and autumn trapping sessions as “dry season” and the 7-month period (October–April) between autumn and spring trapping sessions as “wet season.” We tested for the influence of the following covariates on pocket mice demographics: (1) average seasonal atmospheric temperature; (2) total seasonal precipitation; (3) coefficient of variation (CV) of average seasonal temperature and total seasonal precipitation; (4) a one-season lag in total precipitation and its CV to account for the delayed response of populations to precipitation; and (5) regional temperature and precipitation oscillations caused by El Niño. All climatic covariates were standardized to a mean of zero and a SD of 1 (Schroeder et al. 2016).

We used atmospheric temperature and rainfall data recorded at the National Oceanographic and Atmospheric Agency’s (NOAA) Paso Robles City weather station (35.66°N, 120.69°W) situated 11.7 km from the study area (National Oceanographic and Atmospheric Administration 2016). Seasonal averages were computed using monthly data. We tested for effects of El Niño on demographic parameters of California pocket mouse using monthly values of Oceanic Niño Index (ONI). This index tracks average sea-surface temperature in the equatorial Pacific Ocean. El Niño conditions occur when the average sea-surface temperature of three consecutive months is 0.5°C above average temperature and La Niña conditions occur when the average sea-surface temperature is 0.5°C below average temperature. We obtained the ONI value from the National Oceanographic and Atmospheric Agency Climate Prediction Center ([www.cpc.noaa.gov/products/analysis\\_monitoring](http://www.cpc.noaa.gov/products/analysis_monitoring)).

**Data analysis.**—Capture-mark-recapture models have been used extensively for estimating survival, recruitment, and

population growth rates of small mammals (Lima et al. 2003; Kelt 2011). The models require encounter history data from repeated sampling of individually marked animals, thereby accounting for animals that although present on the study site, might not be detected in all successive trapping sessions. We used the  $\phi$ - $f$  parameterization of Pradel’s CMR model because this approach permitted simultaneous estimation of recapture probability ( $p$ ),  $\phi$ , and  $f$ , in a single likelihood (Pradel 1996). We used an all-combination modeling strategy (Doherty et al. 2012) to estimate  $p$ ,  $\phi$ , and  $f$  and to test for the influence of time (i.e., trapping sessions), sex, and season (wet or dry season), and climatic covariates (only on  $\phi$  and  $f$ ) on aforementioned parameters. We specifically tested for (1) singular, additive, and interactive effects of time, sex, and season on  $p$ ; (2) singular effects of environmental covariates (one variable at a time) on  $\phi$  and  $f$ ; and (3) additive and interactive effects of climatic covariates, sex, and season on  $\phi$  and  $f$  (Table 1). Because several climatic covariates were highly correlated, we did not test for additive or interactive effects of  $\geq 2$  climatic covariates in the same model (Supplementary Data SD1). We estimated overall, sex-specific, seasonal, and time-specific estimates of the realized  $\lambda$  using the  $\phi$ - $\lambda$  parameterization of Pradel’s CMR model; we included top model for  $\phi$  from  $\phi$ - $f$  parameterization and overall sex-specific, seasonal, and time-specific effects on  $\phi$  (Pradel 1996; Williams et al. 2002; Nichols 2016).

We undertook all CMR analyses using program MARK (White and Burnham 1999) version 6.2 accessed using the RMark package (Laake and Rexstad 2008) for the R programming language (R Development Core Team 2020). We carried out the RELEASE (test 2 and 3) goodness-of-fit (GOF) test to test the null hypothesis that the general time-dependent Cormack–Jolly–Seber model fits our data using the *release.gof* function in RMark (Burnham et al. 1987, 2011). GOF test tests for the violation of the assumption that every marked animal has the same probability of capture, there is no tag loss, and that animals marked during any instance have an equal probability of survival (Burnham et al. 1987). We used an information-theoretic approach for model selection and statistical inference, based on Akaike Information Criteria corrected for small sample size (AIC<sub>c</sub>—Burnham et al. 1987, 2011). We considered

**Table 1.**—Model comparison presenting the top five models estimating recapture probability ( $p$ ), survival probability ( $\phi$ ), and recruitment rate ( $f$ ) and testing for the influence of time (i.e., trapping sessions), sex, season (wet season, May–October or dry season, November–April), and climatic covariates (only on  $\phi$  and  $f$ ) on the aforementioned parameters of the California pocket mouse (*Chaetodipus californicus*), at Camp Roberts, California. The table lists the number of parameters ( $K$ ), Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), the difference in AIC<sub>c</sub> value from the best-supported model ( $\Delta$ AIC<sub>c</sub>), and the relative model probability (weight) for the five best-supported models. Additive effects are indicated by a “+,” and additive and interactive effects are indicated by “\*.” Models were ranked based on the AIC<sub>c</sub> values.

Model	$K$	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	Weight
$\phi(\text{rain\_cv\_onelag}^a * \text{season}) p(\text{time}) f(\text{rain\_sum\_onelag}^b * \text{season})$	28	8000.16	0.00	0.84
$\phi(\text{rain\_cv\_onelag} + \text{sex} * \text{season}) p(\text{time}) f(\text{rain\_sum\_onelag} * \text{season})$	29	8004.45	4.28	0.10
$\phi(\text{rain\_cv\_onelag} + \text{season}) p(\text{time}) f(\text{rain\_sum\_onelag} * \text{season})$	27	8007.30	7.14	0.02
$\phi(\text{rain\_cv\_onelag} + \text{sex} + \text{season}) p(\text{time}) f(\text{rain\_sum\_onelag} * \text{season})$	28	8008.01	7.84	0.02
$\phi(\text{rain\_cv}^c * \text{sex}) p(\text{time}) f(\text{rain\_sum\_onelag} * \text{season})$	28	8009.21	9.05	0.01

<sup>a</sup>rain\_cv\_onelag = coefficient of variation (CV) of seasonal rainfall from the season prior to capture.

<sup>b</sup>rain\_sum\_onelag = total seasonal rainfall from the season prior to capture.

<sup>c</sup>rain\_cv = coefficient of variation (CV) of rainfall during season of capture.

models within  $\Delta AIC_c$  of 2 to be equivalent. Overall, sex, and season-specific estimates of demographic parameters were based on the most parsimonious model testing for the constant, sex, and season-specific effect on the demographic parameter. Covariate effects on  $\phi$  or  $f$  were considered to be substantial if the associated 95% confidence interval of the corresponding slope parameter does not include zero (Grosbois et al. 2008; Hardouin et al. 2014). Significance of the influence of climatic covariates on demographic parameters was assessed using an analysis of deviance (ANODEV), and the proportion of variance in  $\phi$  and  $f$  explained by a climatic covariate was estimated using  $R_{dev}^2$  (Grosbois et al. 2008; Gimenez and Barbraud 2017):

$$R_{dev}^2 = \frac{\text{deviance}_{\text{constant model}} - \text{deviance}_{\text{covariate model}}}{\text{deviance}_{\text{constant model}} - \text{deviance}_{\text{time-dependent model}}},$$

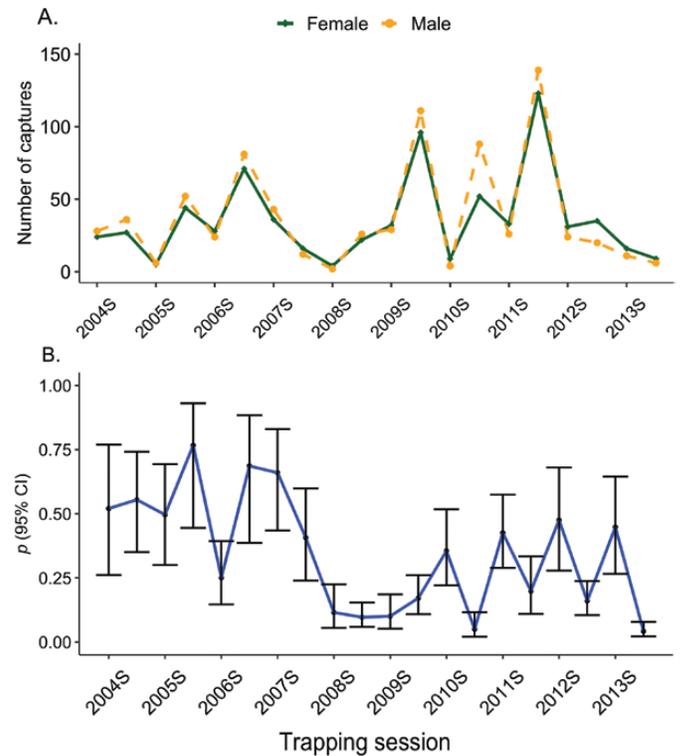
where  $\text{deviance}_{\text{constant model}}$  refers to the deviance of the null model for the parameter being tested while holding other parameters at the general structure (time-specific),  $\text{deviance}_{\text{covariate model}}$  refers to the deviance of the model testing for the influence of the covariate of the parameter being tested while holding other parameters at the general structure (time-specific), and  $\text{deviance}_{\text{time}}$  refers to all the parameters at the general structure (time-specific).

## RESULTS

Our trapping effort (84,288 trap nights) yielded 2,005 captures of 1,374 unique California pocket mice. Although slightly more males (714) than females (660) were captured (Fig. 2A), the sex ratio of captured mice did not deviate from parity ( $\chi^2 = 2.04$ ,  $d.f. = 1$ ,  $P = 0.15$ ). Average age of captured California pocket mice was  $\leq 1$  year. The GOF test revealed no evidence of a lack of fit ( $\chi^2 = 20.45$ ,  $d.f. = 33$ ,  $P = 0.95$ ). We captured fewer mice in spring (191 females and 168 males) than in autumn (469 females and 546 males). Recapture probability ( $p$ ) during the study varied with time (Supplementary Data SD2; Fig. 2B).

Overall  $\phi$  and  $f$  (estimated based on the most parsimonious  $\phi(\cdot)$  and  $f(\cdot)$  models) was  $0.76 \pm 0.01$  and  $0.17 \pm 0.01$ , respectively (Supplementary Data SD3A). Based on the most parsimonious model testing for the effect of sex and season on  $\phi$  and  $f$  (Supplementary Data SD3B), we found that  $\phi$  did not differ between sexes (males =  $0.77 \pm 0.01$ ; females =  $0.76 \pm 0.01$ ); it was slightly higher during dry season than wet season (dry season:  $0.79 \pm 0.02$ ; wet season:  $0.74 \pm 0.01$ ). On the other hand,  $f$  varied strongly across seasons, with substantially higher  $f$  during dry season ( $0.39 \pm 0.04$ ) than wet season ( $0.09 \pm 0.02$ ). Overall  $\lambda$  was  $1.00 \pm 0.002$  (estimated from the most parsimonious  $\lambda(\cdot)$  model) for the entire study period, but it varied with time (Fig. 3; for additional details, Supplementary Data SD4).

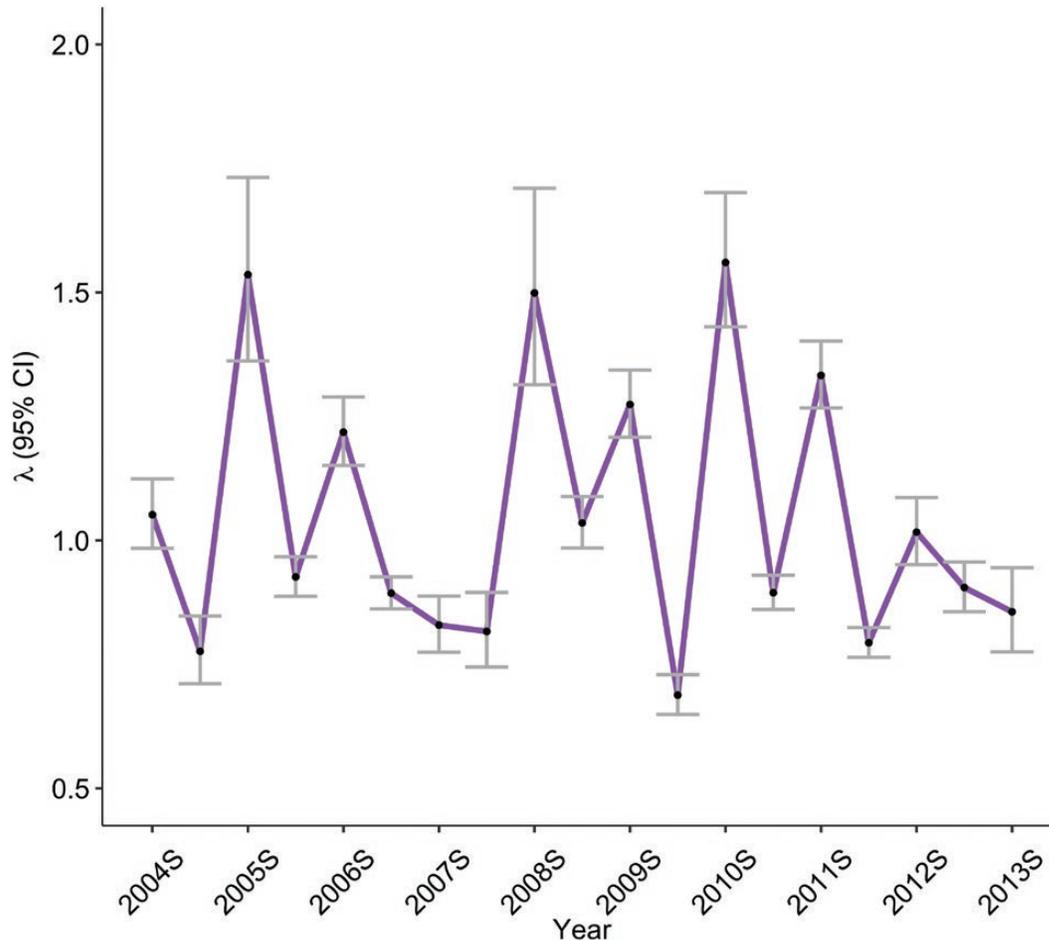
The most parsimonious overall model included an interaction effect of season and CV of rainfall (with a one-season lag) on  $\phi$  and an interaction effect of season and total seasonal rainfall (with a one-season lag) on  $f$  (Table 1; Supplementary Data SD2). Based on this model, the CV of rainfall (with a one-season lag) positively influenced  $\phi$ ; the effect was stronger during the



**Fig. 2.**—A) Total number of male and female California pocket mice (*Chaetodipus californicus*) captured during each of the 20 trapping sessions during the 10 years of the study (2004–2013). The first four numbers in the x-axis label are the year of the trapping session, followed by the season of trapping session (S = spring; May trapping session). B) Estimates of recapture probability ( $p$ ) and 95% CI for California pocket mice (*Chaetodipus californicus*) captured over the 20 trapping sessions at Camp Roberts, California, in 2004–2013. Estimates are derived from the top model (Table 1). The first four numbers in the x-axis label are the year of the trapping session, followed by the season of trapping session (S = “spring”; May trapping session).

dry season than the wet season (Fig. 4A). Total seasonal rainfall (with a one-season lag) positively affected  $f$  during dry season; the effect was weak and in the opposite direction during wet season (Fig. 4B).

Analysis of individual climatic covariate effects revealed that  $\phi$  was positively influenced by the average seasonal temperature, CV of temperature, CV of rainfall (with and without a one-season lag), and El Niño index, and negatively influenced by total seasonal rainfall because associated 95% confidence intervals of the corresponding slopes did not include zero for these covariates. Proportions of variation explained by individual climatic covariates were generally small ( $R_{dev}^2 \leq 20\%$ ), with total seasonal rainfall being the most influential climatic variable (Table 2). Recruitment rate was positively influenced by total seasonal rainfall (with a one-season lag), average seasonal temperature, and CV of rainfall and temperature (Table 2) and was negatively influenced by the CV of rainfall (with a one-season lag), total seasonal rainfall (without a one-season lag), and El Niño index. Among climatic covariates we considered, total seasonal rainfall (with a one-season lag) was the most influential and explained 51% of the variation in  $f$  (Table 2).



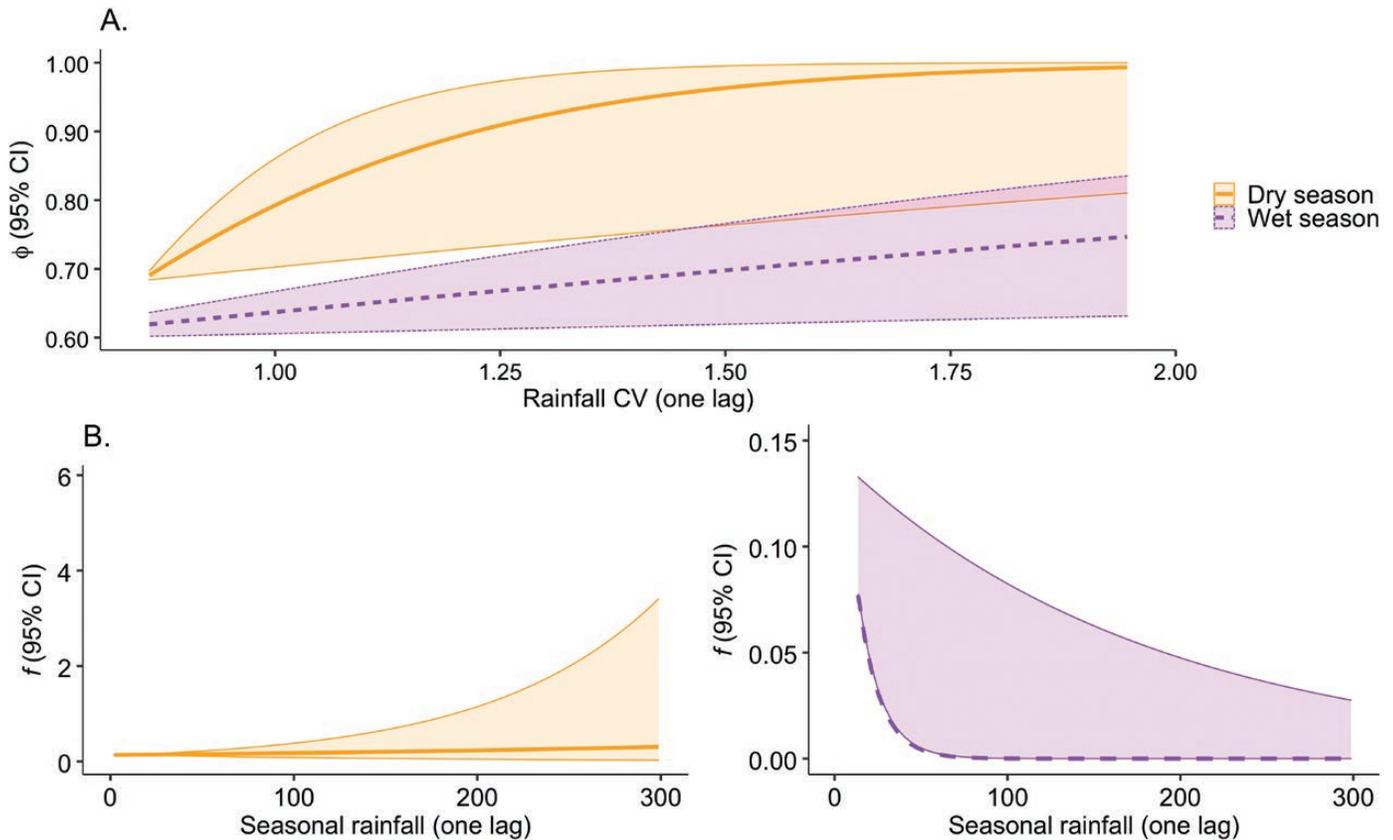
**Fig. 3.**—Estimates for May trapping session of realized population growth rate ( $\lambda$ ) and 95% CI for California pocket mice (*Chaetodipus californicus*), 2004–2013, at Camp Roberts, California. Estimates are derived from the most parsimonious Pradel’s survival ( $\phi$ )– $\lambda$  model (Supplementary Data SD4). The first four numbers in the x-axis label are year of the trapping session, followed by the season of trapping session (S = spring; May trapping session).

## DISCUSSION

As is the case in many small mammal species, population dynamics and factors driving these have been largely unknown for the California pocket mouse. This is particularly concerning in light of human-caused habitat alternations, the alarming frequency of intense wildfires, and rapidly changing weather patterns that are occurring within the distributional range of California pocket mouse. Our estimates of the vital rates of the California pocket mouse, and how these rates were affected by climatic factors during a 10-year study in coastal-central California, provides a starting point in the understanding of how populations of this little-known species will respond to these disruptions. When monitored over time, this species can serve as an indicator of the climate change–induced alteration of the fragile and sensitive ecological system it occupies.

Similar to many closely related species, such as the long-tailed pocket mouse (*Perognathus formosus*), little pocket mouse (*P. longimembris*), and Pacific pocket mouse (*P. longimembris pacificus*—Kenagy and Bartholomew 1985), the California pocket mouse gives birth only once a year in April – July (dry season). Spring captures (191

females and 168 males) were only one-third of autumn captures (469 females and 546 males), indicating that the abundance of California pocket during spring sampling was lower than during autumn sampling. The single breeding event in spring – summer explains a larger number of mice captured in autumn than in spring, as well as the high monthly recruitment rate of 0.39 during the dry season. The strong positive effect of temperature on recruitment (measured in October) during our study is arguably an artifact of the timing of reproduction. Winter recruitment rate of only 0.09 is due almost entirely to immigration. In contrast, the San Diego pocket mouse (*C. fallax*) can breed throughout the year if rainfall conditions are favorable (McClenaghan 1983). Our study does not provide evidence that high total seasonal rainfall influenced the number of breeding events of the California pocket mouse. The positive effect we documented of total seasonal rainfall (with a one-season lag) on recruitment (Fig. 4B) was manifested in several ways. Cover and edible seeds produced during a wet winter undoubtedly help females survive winter when food is scarce, and winter rainfall puts females in good condition going into the spring–summer breeding season. During a dry year, higher winter rainfall



**Fig. 4.**—A) Influence of the coefficient of variation of the CV of rainfall (with a one-season lag; “Rainfall CV (one lag)”) on apparent survival ( $\phi$ ), and B) influence of total seasonal rainfall (with a one-season lag; “Seasonal rainfall (one lag),” measured in “mm”) on the recruitment rate of the California pocket mouse population (*Chaetodipus californicus*) during the dry season (left panel) and wet season (right panel) in 2004–2013 at Camp Roberts California. These relationships are based on the most parsimonious model (Table 1, model 1). Also depicted in both panels are 95% CI.

could further boost fecundity by bringing a greater proportion of females into breeding condition. California pocket mice do not breed during winter; therefore, the negative effect of rainfall during winter simply indicates reduced immigration during wet winters (Fig. 4B).

While total seasonal rainfall boosts recruitment by its positive effect on plant production and the condition of females going into the breeding season, our results show a negative effect on recruitment of total seasonal rainfall (without a lag) and El Niño storms during winter and early spring (Table 2). Heavy rain can cause fungal infections of critical seed stores during winter (Reichman et al. 1985) and direct mortality from flooding of natal burrows during the spring breeding event (Thibault and Brown 2008). Monthly overall survival of pocket mice in our study was relatively high (76%), and was slightly higher in dry season ( $0.79 \pm 0.02$ ) than in wet season ( $0.74 \pm 0.01$ ). A higher CV of rainfall (with a one-season lag) was correlated with higher survival (Fig. 4A). CV of temperature also had a positive influence on survival probability of California pocket mouse. In a semiarid region such as our study area where mean summer rainfall is already low, variability in rain could manifest as more days or months with even less precipitation or more days or months with more (Boyce et al. 2006). During our study, the latter potentially benefited survival.

Although average seasonal temperature positively influences survival of the California pocket mouse, it explained only a small proportion of variance in survival (Table 2). This result is in contrast to the strong negative effect of average seasonal temperature on survival rates of the California mouse (*Peromyscus californicus*—Tietje et al. 2018), the piñon mouse (*P. truei*—Srivathsa et al. 2019), and the brush mouse (*P. boylii*—Polyakov et al. 2021) in the same study area. These species-specific differences might reflect several adaptations of the California pocket mouse to ameliorate potentially negative effects of high temperature on survival. California pocket mice can survive without free water (Tucker 1962). Herbaceous plant seeds, its primary food, are relatively persistent during dry season, and seeds are appropriate for caching. The burrow ameliorates temperature extremes (Tucker 1966), and thermoregulation further maintained because pocket mice are known to occlude entrances to their burrows (French 1977). Aboveground activity is restricted essentially to food gathering and mate finding. During a food shortage, they can enter diurnal torpor where the energy required to maintain a stable weight is reduced by almost one-half (43%—Tucker 1962, 1965, 1966). Tucker (1966) surmised that torpor is an adaptation to the variable climate of California, particularly seasonally available foods.

**Table 2.**—Influence of climatic covariates on monthly survival probability ( $\phi$ ) and recruitment rate ( $f$ ) of California pocket mice (*Chaetodipus californicus*) at Camp Roberts, California, using time-specific recapture probability. A “+” and “–” indicate the prediction of the positive or negative influence of the climatic covariate on the population parameter, respectively. For both  $\phi$  and  $f$ , the estimate of the slope parameter ( $\beta$ ), along with the upper (UCL) and lower (LCL) 95% CI, and the model used to estimate the parameter values are reported. Proportion of variation in a demographic parameter explained by a climatic covariate ( $R_{dev}^2$ ) is also reported, along with  $F$ -statistics, degrees of freedom, and  $P$ -values.

Covariate <sup>a</sup>	Expected slope of $\beta$	$\beta$ (LCL, UCL)	
		$R_{dev}^2$ ( $F_{d,f,1, d,f,2}, P$ ) (Model)	
		$\phi$	$f$
Average seasonal temperature (temp_avg <sup>a</sup> )	$\phi$ and $f$ : – availability of resources will decrease with increasing temperature reducing both survival and recruitment	0.07 (0.06, 0.09) $R_{dev}^2 = 2.17\%$ ( $F_{1,17} = 35.26, P < 0.001$ ) $\phi$ (temp_avg) $p$ (time) $f$ (time)	0.35 (0.12, 0.57) $R_{dev}^2 = 17.03\%$ ( $F_{1,17} = 3.49, P = 0.07$ ) $\phi$ (time) $p$ (time) $f$ (temp_avg)
Coefficient of variation of average temperature (temp_cv <sup>b</sup> )	$\phi$ and $f$ : – greater variability in temperature can negatively influence both survival and recruitment	0.13 (0.11, 0.15) $R_{dev}^2 = 4.22\%$ ( $F_{1,17} = 36.38, P < 0.001$ ) $\phi$ (temp_cv) $p$ (time) $f$ (time)	0.24 (0.12, 0.37) $R_{dev}^2 = 7.02\%$ ( $F_{1,17} = 1.28, P = 0.27$ ) $\phi$ (time) $p$ (time) $f$ (temp_cv)
Total seasonal rainfall (rain_sum <sup>c</sup> )	$\phi$ and $f$ : + food and water availability will be higher, increasing both $\phi$ and $f$	–0.28 (–0.31, –0.25) $R_{dev}^2 = 19.15\%$ ( $F_{1,17} = 4.02, P = 0.06$ ) $\phi$ (rain_sum) $p$ (time) $f$ (time)	–0.81 (–0.88, –0.75) $R_{dev}^2 = 2.42\%$ ( $F_{1,17} = 0.42, P = 0.52$ ) $\phi$ (time) $p$ (time) $f$ (rain_sum)
Coefficient of variation of seasonal rainfall (rain_cv <sup>d</sup> )	$\phi$ and $f$ : – greater variability in precipitation can negatively influence both survival and recruitment	0.30 (0.26, 0.35) $R_{dev}^2 = 15.13\%$ ( $F_{1,17} = 43.25, P < 0.001$ ) $\phi$ (rain_cv) $p$ (time) $f$ (time)	0.26 (0.02, 0.49) $R_{dev}^2 = 7.12\%$ ( $F_{1,17} = 1.30, P = 0.26$ ) $\phi$ (time) $p$ (time) $f$ (rain_cv)
Coefficient of variation of seasonal rainfall with one-season lag (rain_cv_onelag <sup>e</sup> )	$\phi$ and $f$ : – greater variability in precipitation can negatively influence both survival and recruitment	0.10 (0.09, 0.12) $R_{dev}^2 = 6.05\%$ ( $F_{1,17} = 37.42, P < 0.001$ ) $\phi$ (rain_cv_onelag) $p$ (time) $f$ (time)	–0.39 (–0.71, –0.07) $R_{dev}^2 = 14.74\%$ ( $F_{1,17} = 2.93, P = 0.10$ ) $\phi$ (time) $p$ (time) $f$ (rain_cv_onelag)
Total seasonal rainfall with one-season lag (rain_sum_onelag <sup>f</sup> )	$\phi$ and $f$ : + greater resource availability can have delayed positive effect on survival and recruitment	0.002 (0, 0.005) $R_{dev}^2 = 0.01\%$ ( $F_{1,17} = 34.21, P < 0.001$ ) $\phi$ (rain_sum_onelag) $p$ (time) $f$ (time)	0.08 (0.06, 0.07) $R_{dev}^2 = 51.0\%$ ( $F_{1,17} = 17.69, P < 0.001$ ) $\phi$ (time) $p$ (time) $f$ (rain_sum_onelag)
El Niño <sup>g</sup>	$\phi$ and $f$ : + increased rainfall associated with El Niño can increase resource availability	0.22 (0.20, 0.25) $R_{dev}^2 = 18.35\%$ ( $F_{1,17} = 45.63, P < 0.001$ ) $\phi$ (El Niño) $p$ (time) $f$ (time)	–0.17 (–0.17, –0.17) $R_{dev}^2 = 3.70\%$ ( $F_{1,17} = 0.65, P = 0.42$ ) $\phi$ (time) $p$ (time) $f$ (El Niño)

<sup>a</sup>temp\_avg = average seasonal temperature during season of capture.

<sup>b</sup>temp\_cv = coefficient of variation (CV) of average temperature during season of capture.

<sup>c</sup>rain\_sum = total rainfall during season of capture.

<sup>d</sup>rain\_cv = coefficient of variation (CV) of rainfall during season of capture.

<sup>e</sup>rain\_cv\_onelag = coefficient of variation (CV) of seasonal rainfall from the season prior to capture.

<sup>f</sup>rain\_sum\_onelag = total seasonal rainfall from the season prior to capture.

<sup>g</sup>El Niño = Oceanic El Niño index.

The population of California pocket mice in our study system was stable, perhaps due to the coping strategies discussed above, and extremes and variations in temperature and rainfall that occur in our study area were tolerated by the population of California pocket mice. Nevertheless, predictions call for changes in regional climatic patterns, particularly changes in precipitation patterns (Knapp et al. 2008; Scheffers et al. 2016). Climate studies indicate that much of the distribution of the pocket mouse will face enhanced El Niño – La Niña oscillations (Lenihan et al. 2008) that will lead to episodes of

extreme rainfall events within periods of more intense and prolonged drought. Rowe et al. (2015) documented the response of 34 species of small mammals to changes in weather patterns that occurred the past century in montane forests within or nearby Yosemite National Park, California. The California pocket mouse was one of the 25 species that shifted its occurrence along the elevational gradient (Rowe et al. 2015). Nonetheless, Rowe et al. (2015) concluded that several biotic factors (natural habitat succession, competition among species, and invasive species) drove many of the distributional shifts

they documented, and they predicted that human-mediated habitat alterations would have more influence on the demographics and distributions of small mammals in California than would changing weather patterns. Widespread and rapid alterations of habitat in the past decades within the distribution of the California pocket mouse suggest that this may be the case.

Movement of humans into wildlands has greatly increased frequency of wildfires in California's already fire-prone Mediterranean climate (Keeley and Fotheringham 2001; Lenihan et al. 2008). An experimental fire that we carried out in 1997 on our study site at Camp Roberts did not affect California pocket mouse abundance and, as a matter of fact, survival was marginally higher following the fire (Tietje et al. 2018); however, this low-intensity burn had no appreciable effect on shrub or tree cover. In contrast, Brehme et al. (2011) reported that a population of the congeneric San Diego pocket mouse (*C. fallax fallax*) decreased in response to wildfire. They attributed the decrease to the large reduction of protective cover and competitive advantage obtained following the fire by a generalist species, the deer mouse (*P. maniculatus*). Diffendorfer et al. (2012) documented consistently reduced numbers of California pocket mice following each of several episodes of heavy rainstorms in winter that followed a large wildfire in southern California—perhaps not unlike the effects of El Niño on recruitment in our study. Species-specific response to wildfire also depends on the habitat type (Schwilk and Keeley 1998). Movement of humans into shrublands in the especially southern half of the California pocket mouse distribution (Fig. 1) is increasing the occurrence and size of areas known as “urban–wildland interface.” In these areas, small mammal residents might respond strongly to the human disturbance-related vegetation changes (Bolger et al. 1997; Sauvajot et al. 1998). Those authors documented reduced numbers of small mammals due to shrub habitat alterations, including numbers of the California pocket mouse. Sauvajot et al. (1998:293) concluded that “... urban-associated habitat fragmentation and disturbance can lead to small mammal extinctions.”

Of concern from the San Francisco Bay to Big Sur, the exotic pathogen *Phytophthora ramareoren*, the causal agent of sudden oak death (SOD), has killed an estimated 50 million tanoak trees (*Notholithocarpus densiflorus*; <http://www.suddenoakdeath.org/>) and up to five million coast live oak trees (*Quercus agrifolia*; M. M. Garbelotto, University of California, Berkeley, pers. comm.). In parts of southern California, the gold spotted oak borer (*Agrilus auroguttatus*—Coleman and Seybold 2008) has killed thousands of coast live oak trees (Das et al. 2020). These authors documented drought-induced mortality of blue oak (*Q. douglasii*) in oak woodland of Yosemite National Park, California, undoubtedly also the cause of oak mortality oftentimes reported by the concerned public and citizen scientists from throughout the distribution of the California pocket mouse. Effects of tree mortality on small mammals have not been studied extensively; however, some evidence exists that a decrease in structural complexity of the habitat leads to a decline in abundances of small mammals (Smit et al. 2001)

and makes them more vulnerable to predator-induced mortality (Torre and Diaz 2004).

Short-lived and annually reproducing species such as California pocket mouse exhibit high sensitivity to temporally correlated environmental conditions, and their short generation time might allow them to adapt rapidly to changing environmental optimum (Morris et al. 2008; Paniw et al. 2018; Postuma et al. 2020). For the same reason, they also suffer large population declines when the environmental optimum shifts, which is expected due to global environmental changes (Postuma et al. 2020). Our 10-year study provides the first estimates of demographics of this barely studied species and concludes that the population is relatively stable with a long-term population growth of ~1.0 on the study site, a mostly undisturbed habitat. Our results show that the California pocket mouse is quite tolerant of dry and hot conditions. Perhaps due to its life-history strategies and coping strategies (e.g., food caching, predominantly seed diet, and ability to enter torpor), it has evolved to deal with the seasonal environment that may become more seasonal due to climate change. If conditions become wetter and more variable, our results suggest that California pocket mouse will have higher survival and recruitment.

We note, however, that we did not consider several abiotic and biotic variables (e.g., competition, predation) that could potentially influence California pocket mouse population dynamics. We also do not know the extent to which our results can be applied to conditions other than those that occurred during our study, which was carried out in a relatively undisturbed habitat. Trends for other populations of the California pocket mouse could be different because these dynamics will vary with local climatic conditions, vegetation structure, fire regimes, space, and intensity of anthropogenic disturbance. Future studies from other regions of California and Baja California are needed to understand population dynamics of California pocket mice and the effects of abiotic and biotic factors on these dynamics from across the distribution of the species.

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### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Pairwise correlation plot for continuous climatic covariates.

**Supplementary Data SD2.**—Full model comparison table testing for the effect of time, and an additive effect of time and sex on recapture probability ( $p$ ); season (wet season or dry season), sex (male or female), climatic covariates, and additive and interactive effects of sex and season with individual climatic covariates on survival probability ( $\phi$ ) and recruitment rate ( $f$ ) of California pocket mouse (*Chaetodipus californicus*).

**Supplementary Data SD3.**—Models used to estimate (A) overall and (B) sex and season-specific survival probability ( $\phi$ ) and recruitment rate ( $f$ ) of California pocket mouse (*Chaetodipus californicus*).

**Supplementary Data SD4.**—Model comparison table testing for the effect of time, season (wet season or dry season), sex (male or female), and additive and interactive effects of time, sex, and season on population growth rate ( $\lambda$ ) of California pocket mouse (*Chaetodipus californicus*).

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