Climatic factors and population demography in big-eared woodrat, *Neotoma macrotis*

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Changes in temperature and rainfall patterns can have marked impacts on small mammal populations that inhabit environments with highly fluctuating water availability. With projected increases in droughts and fewer but more intense rainfall events in the Southwestern United States, the persistence of many wildlife populations may be threatened. Our goal was to assess how temperature and rainfall during distinct dry and wet seasons influenced the dynamics of a population of big-eared woodrats (*Neotoma macrotis*) in a mixed oak woodland of coastal central California. We applied Pradel's temporal symmetry models to our 21-year biannual capture–mark–recapture data set (1993–2014) to determine the effects of climatic factors on the woodrats' apparent survival (Φ) and recruitment rate (*f*). Monthly Φ averaged 0.945 ± 0.001 and varied with season. Monthly *f* was 0.064 ± 0.001 in the wet season (*f* was fixed to 0 in the dry season). Monthly population growth rate (λ) varied from 0.996 ± 0.001 during the dry season to 1.001 ± 0.001 during the wet season, which indicated a stable population (0.999 ± 0.001). Total rainfall from the previous season and mean temperature during the same season positively influenced Φ and *f*. By contrast, Φ and *f* were negatively influenced by mean temperature from the previous season and total rainfall in the same season. The resulting λ fluctuated with total rainfall, particularly in the wet season. Our results suggest that the big-eared woodrat population may not be substantially affected by warm temperatures per se, potentially because of the microclimate provided by its stick houses. We also discuss its adaptability to local food resources and relatively slow life history relative to other cricetids, and propose that the big-eared woodrat population may be equipped to cope with future climate change.

Key words: apparent survival, climate change, delayed climatic effect, population growth rate, rainfall, recruitment rate, seasonality, temperature

Last century's increase of only 1°C in global temperature has substantially impacted the morphology, distribution, population dynamics, and interspecific interactions of organisms worldwide (Scheffers et al. 2016). Terrestrial and aquatic ecosystems are under stress, and some have already shifted to a new state (e.g., Alaskan tundra losing ground to boreal forest—Scheffers et al. 2016). Future climate projections include further temperature increases, more variable rainfall patterns, and more frequent and prolonged droughts (Smith et al. 2015; IPCC 2018). In the United States, future climate alterations likely will be especially pronounced in the Southwest (Garfin et al. 2013). In environments where water availability and the biomass of some

plant material (e.g., mast, leaves of deciduous plants) fluctuate greatly, climate change almost certainly will affect the diversity, structure, and function, of ecological communities; however, the direction and magnitude of such effects mostly are unknown (Chesson et al. 2004; Schwinning and Sala 2004).

Droughts reduce annual plant production and palatability, which can adversely affect survival (Moreno and Møller 2011) and reproduction of small mammals (e.g., Smith 1995; Armitage 2013), and potentially contribute to local extinctions of rodent populations (Gillespie et al. 2008). However, many species of rodents, especially those with high reproductive output and short life span (e.g., Sigmodontinae—Weir 1974),

have adapted to unpredictable water and food resources. When sustained heavy rainfalls follow long periods of drought, even longer-lived rodents with relatively lower reproduction (e.g., Caviomorpha) can recover within a year or two (Jaksic 2001; Bradley et al. 2006; Thibault et al. 2010; Greenville et al. 2012). Furthermore, some *Neotoma* species adapted to historic climate extremes that occurred during the late Pleistocene epoch (40,000 BP) and into the early Holocene (Smith and Charnov 2001; Smith and Betancourt 2003). These suggest a high resilience to climatic variability. However, the current pace of climate change may not allow enough time for adaptive responses to evolve, at least for some species (M'Closkey 1972; Gillespie et al. 2008; Kelly et al. 2013). In addition, ambient warming may reduce some species' ability to metabolize dietary toxins and affect their foraging behavior, as suggested for the white-throated woodrat (*N. albigula*—Dearing et al. 2008). Therefore, it is essential to understand species-specific responses to climatic variability before formulating long-term conservation plans for species that may be affected by global climate change.

Our objectives were to (1) quantify the population dynamics of a big-eared woodrat (*N. macrotis*) population in coastal central California, and (2) assess the influence of climatic variables on the realized population growth rate and its constituent vital rates: apparent survival and recruitment. To achieve our objectives, we applied Pradel's temporal symmetry capture–mark–recapture models to a 21-year data set and tested for the seasonal effects of local climatic variables (rainfall and temperature). Because of the pulsed nature of rainfall in this system, with alternating dry and wet seasons in the big-eared woodrat range and the effects of rainfall on small mammal populations (Gillespie et al. 2008; Greenville et al. 2012), we predicted that rainfall-mediated recruitment would primarily drive the dynamics of our study population.

The big-eared woodrat is an excellent model species to test for climatic effects on population dynamics for several reasons. First, little is known about the big-eared woodrat as a distinct species, including its demography (Feldhamer and Poole 2008; but see Matocq 2004; Lee and Tietje 2005), because it only was recognized recently as a species distinct from the dusky-footed woodrat (*N. fuscipes*—Matocq 2002). Second, although we understand the population dynamics of *Peromyscus* spp. in the same community (Tietje et al. 2018; Srivathsa et al. 2019), woodrats have different life history traits and likely respond differently to climatic factors. Third, big-eared woodrat numbers decline substantially during drought (Linsdale and Tevis 1956; Spevak 1983), and they can be adversely affected by heavy rainfall (Linsdale and Tevis 1956), demonstrating their susceptibility to climatic variability. Fourth, many woodrat species, including big-eared woodrats, are capable of metabolizing toxic secondary plant compounds and have adapted a specialized diet (Atsatt and Ingram 1983; Dial 1988; McEachern et al. 2006; Haley et al. 2007a, 2007b; Dearing et al. 2008). Finally, in at least two woodrat species (*N. albigula* and *N. lepida*), as body temperature increases with ambient warming, the ability to metabolize dietary toxins is reduced, and foraging behavior affected (Dearing et al. 2008; Kurnath et al. 2016).

Materials and Methods

Study Species

Big-eared woodrats occur in mesic oak and chaparral woodlands from Monterey Bay into Baja California, across the Transverse Ranges, and within the Sierra Nevada Ecoregion (Fig. 1). Because big-eared woodrats only recently were distinguished from dusky-footed woodrats (Matocq 2002), we used dusky-footed woodrat studies to describe big-eared woodrat life history traits. The species is mostly active at night (English 1923). Principal food items are leaves of coffeeberry (*Frangula californica*) and of coast live oak (*Quercus agrifolia*), both of which are available year-round (Vestal 1938; Hunter et al. 2017). In addition to leaves, big-eared woodrats also feed on acorns, the availability of which varies with rainfall in the previous year (Koenig et al. 1996) and can drive small mammal population dynamics (Elias et al. 2004). The big-eared woodrat diet also includes other herbaceous materials from winter-deciduous plants.

Several studies indicate that population density ranges from one to over 98 individuals per hectare, with individuals living in overlapping clusters (Williams et al. 1992). Female big-eared woodrats within a cluster are not closely related or strongly philopatric as previously reported for the dusky-footed woodrat (Matocq and Lacey 2004). Big-eared woodrats exhibit a mostly promiscuous mating system (Matocq 2004) and breeding occurs during February–September (Carraway and Verts 1991; Matocq 2004), although pregnancies peak in February (Linsdale and Tevis 1951). The gestation period lasts 30–37 days, litters average 2.6 young (range: 1–4), and weaning occurs at 21 days (Carraway and Verts 1991). Most (76%) females produce a single litter per season, but some (24%) give birth to two or more litters within a season (Matocq 2004).

The ambient temperature range within which the woodrat can maintain its body temperature with no additional energy is 20–25°C, with an upper critical limit of 35°C (Lee 1963). Woodrats build dens, called houses, made of sticks, twigs, and bark. The house provides a site for food storage and breeding (English 1923), and protection from predators and extreme temperatures (Carraway and Verts 1991). Predators include snakes, skunks, and raptors (English 1923). On our study site, few woodrats (< 5%) survive > 3 years; most live < 1 year (Lee and Tietje 2005). Based on capture–mark–recapture data collected during this study, the oldest woodrat capture was a female ≥ 6 years old.

Study Area

The Camp Roberts National Guard Post is a 17,000 ha military facility located in coastal central California (Fig. 1). We conducted our study in the 4,500 ha westernmost quarter of the Post, an oak woodland mosaic of grassland, chaparral, and wooded patches. Slopes of 20–30% are common. The climate is Mediterranean, with warm, dry summers and cool, wet winters. Annual precipitation, always as rainfall, is highly variable. Typically, ~95% of rainfall occurs between December and March. During the study (1993–2014), mean total rainfall was
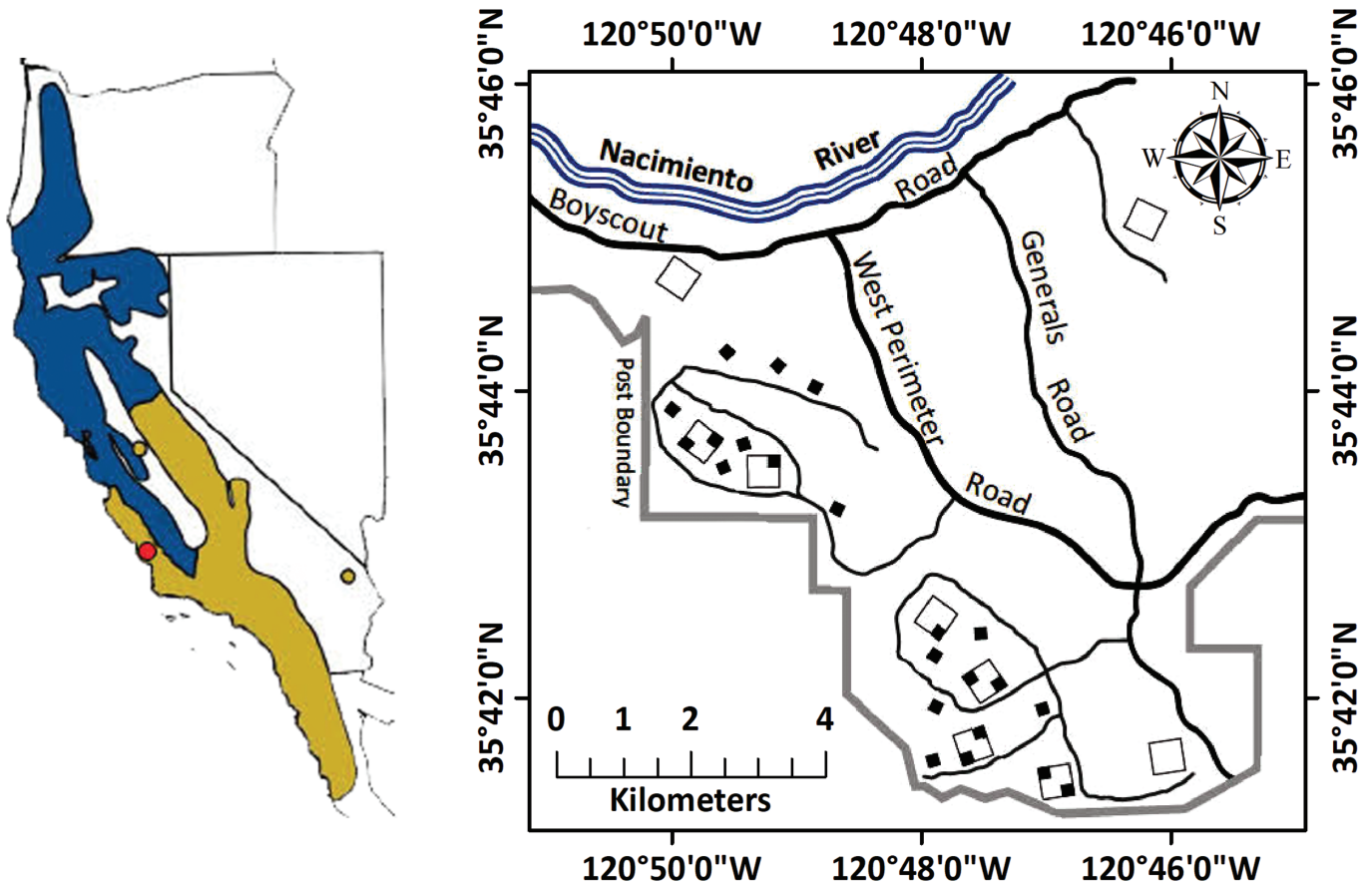
Fig. 1.—Study area at the National Guard Post, Camp Roberts, California. Trapping was carried out on nine 5.8-ha 17 × 17 trapping grids (open, larger squares) from 1993 to 1996, and on twenty-two 1.1-ha 8 × 8 trapping grids (solid, smaller squares) from 1997 to 2014. Left map: location of the study area (solid red circle) and the distributions of *Neotoma fuscipes* (blue) and *N. macrotis* (gold) in central-coastal California, United States. Left map reprinted from Hunter et al. 2017:3899, with permission from Elsevier.

1.63 cm in the dry season (i.e., May to September; range = 0 in 2004 to 5.64 cm in 1998) and 36.8 cm in the wet season (i.e., October to April; range = 15.6 in 2013–2014 to 81.4 cm in 2004–2005).

Wooded patches consisted of pure stands of blue oak (*Q. douglasii*), and on the more mesic sites, a mix of blue oak and coast live oak. The mesic sites included a shrub layer of up to 35% cover and a ground layer of introduced Mediterranean annual grasses (*Avena* and *Bromus* spp.), native bunch grasses (*Nassella* and *Festusca* spp.) and forbs, such as hummingbird sage (*Salvia spathacea*), wild peony (*Paeonia mascula*), and miner's lettuce (*Claytonia perfoliata*). In the shrub layer, toyon (*Heteromeles arbutifolia*), redberry (*Rhamnus crocea*), and coffeeberry predominated with proportionately more buck brush (*Ceanothus cuneatus*) and manzanita (*Arctostaphylos* spp.) on the xeric sites where blue oak dominated the tree canopy. Mediterranean annual grasses comprised the ground layer. Poison oak (*Toxicodendron diversilobum*) formed either a solid blanket of vegetation or scattered patches or stems. Although we trapped big-eared woodrats on all study plots, we captured more woodrats in densely vegetated areas.

Study plots and surrounding areas are largely undisturbed oak woodland. Woodcutting has not occurred and the last wildfire over the study area occurred in 1953. The study area was not used for military training during the study and no disturbance from possible past military training was noticeable. The base has a public hunting program that permits access for hunting of wild turkey (*Meleagris gallopavo*), California quail (*Callipepla californica*), and Columbian black-tailed deer (*Odocoileus hemionus columbianus*) during a weekend in late August, and over the winter holidays. Other than the monitored hunting program, the Post is closed to public access and no shooting or poisoning of animals occurred during our study.

Field Methods

In 1993, we delineated nine 5.8-ha square plots on north-facing or east-facing slopes in areas of ≥ 60% tree canopy cover. On each plot, we established a 17 × 17 grid with 15 m intersections. We marked each plot's 289 intersections with a stake and a survey flag with alphanumeric grid identification. We replaced flags as necessary. In spring 1997, we sampled 10 diagonal 1.1-ha corners (8 × 8 sampling grid) of six of the previously sampled 5.8-ha plots. We also established an additional twelve 1.1-ha plots with 8 × 8 sampling grids in other parts of the study area (Fig. 1). From spring 1997 to spring 2014, we sampled exclusively on the twenty-two 1.1-ha plots.

From fall 1993 to spring 2014, we trapped small mammals for 3–5 nights each spring (May) and fall (October), using one XLK Sherman live trap (7.7 × 8.9 × 30.5 cm; H.B. Sherman Traps, Inc., Tallahassee, Florida) placed within 2 m of each of the grid intersections (see Tietje et al. 2018 for more trapping details). To insulate trapped animals from overnight cool temperatures and early morning heating of the trap by direct sunlight, we placed traps in shade and covered them with grass and other litter from the vicinity of the trap. We baited traps with a mixture of rolled oats, corn, and barley laced with molasses. On initial capture, we placed a uniquely numbered tag (Monel 1005-1L1, National Band and Tag Co., Newport, Kentucky) in the woodrat's right ear, and recorded trap location, tag number, species, sex, mass, and age (juvenile if pelage was all gray to nearly fully molted, or adult if fully molted). We then released animals at site of capture. All trapping and handling of animals followed the guidelines of the University of California, Berkeley, Institutional Animal Care and Use Committee (Permit #R-166) and of the American Society of Mammalogists (Sikes et al. 2016).

Data Analyses

Climatic variables.—Following Tietje et al. (2018) and Srivathsa et al. (2019), for the dry (May–September) and wet (October–April) seasons of 1992–2014, we extracted mean atmospheric seasonal temperature (Temp_avg) and total seasonal rainfall (Rain_sum) using monthly data from the Paso Robles City weather station, located 11.6 km southeast of the study site. We also calculated seasonal coefficient of variation (*CV*) for temperature (Temp_cv) and rainfall (Rain_cv), and considered a one-season lag for all variables (Temp_avg_onelag, Temp_cv_onelag, Rain_sum_onelag, and Rain_cv_onelag; Figs. 2A–D). Although rainfall in coastal central California can be influenced by El Niño-La Niña Oscillations (ENSO— Storlazzi and Griggs 2000), only about a third of El Niño events resulted in high rainfall in the region during the study (Fig. 2E; Null et al. 2017). We therefore did not include ENSO in our analyses. To determine the relative effect of our covariates on demographic parameters from slope estimates, we standardized all variables (Abdi 2007). We also tested for a covariate × season interaction effect on demographic parameters, because the effect of climatic covariates on demographic parameters can vary by season.

Demographic analyses.—We used Pradel's temporal symmetry capture–mark–recapture models (Pradel 1996; Williams et al. 2002; Nichols 2016) to estimate big-eared woodrat recruitment rate (*f*; number of new recruits per individual already in the population through both births and immigration), probabilities of capture (*p*), and apparent survival (Φ; probability that individuals survived and remained on the study site), and to test for the effect of covariates on these parameters. Pradel's model was implemented in Program MARK (White and Burnham 1999) using the RMark package (Laake 2013) for the R computing environment (R Core Team 2015).

We adopted a three-step approach. First, using combinations of time-dependent, season-dependent, and constant parameters, we determined the best general structure for *p*, Φ, and *f*. During preliminary analyses, we encountered severe local convergence issues. To minimize the risk of non-convergence and because the preliminary analysis yielded *f* estimates that were negligible in the dry season, we simplified our models by fixing *f* = 0 during the dry season. We also estimated the parameters at an annual scale, with time intervals set at five-twelfths of a year for the dry season (May to September) and seven-twelfths of a year for the wet season (October to April) corresponding to our trapping sessions. Second, to determine which variable (based on the magnitude of the slope) was associated with the strongest response on demographic parameters, we fitted models with a single weather variable and tested for seasonality by comparing models with independent, additive, and interaction effects with season. For these single-variable models, we used the best *p* structure from step 1. We reported the effect of each tested variable on Φ or *f* using estimates from the best-supported single-variable model (the best-supported model with the tested variable on Φ may include another variable with a different effect on *f*). Finally, because the realized monthly population growth rate (λ) is the sum of Φ and *f*, we determined the response of λ to the covariates found in step 2, using the following equation:

$$\lambda = \frac{e^{a+bX}}{1 + e^{a+bX}} + e^{\alpha+\beta X},$$

where the first and second terms correspond to the back-transformations of Φ (modeled with a logit link) and *f* (modeled with a log link), respectively; *a* and *b* are the beta coefficients for the effect of covariate *X* on Φ; and α and β are the beta coefficients for the effect of the same covariate *X* on *f*. Centered around 1, a λ < 1 indicates a decreasing population, whereas λ > 1 suggests an increasing population.

For all model selections, we used the AICc (Akaike Information Criterion corrected for small samples) and AICc weights to determine the best general or covariate structure of each parameter (Burnham and Anderson 2002). The best model was the model with the lowest AICc and a ΔAICc > 2 from the model with the next lowest AICc. Model averaging was not necessary for our model selection. Because climate data were collected at a seasonal scale and because previous studies on sympatric species on the study area used monthly estimates (Tietje et al. 2018; Srivathsa et al. 2019), we converted all annual estimates to monthly estimates, which we reported ± 1 *SE* using the delta method (Williams et al. 2002). We reported beta coefficients (for slopes and parameter difference between seasons) with 95% confidence intervals to confirm significance.

RESULTS

Our trapping effort totaled ~214,000 trap-nights over 797 nights between October 1993 and April 2014. This effort resulted in 162–1,018 unique captures per trapping session (Fig. 2F) and a total of 35,052 captures of 10,040 big-eared woodrats. On average, individuals were known alive for at least 2.13 ± 1.73
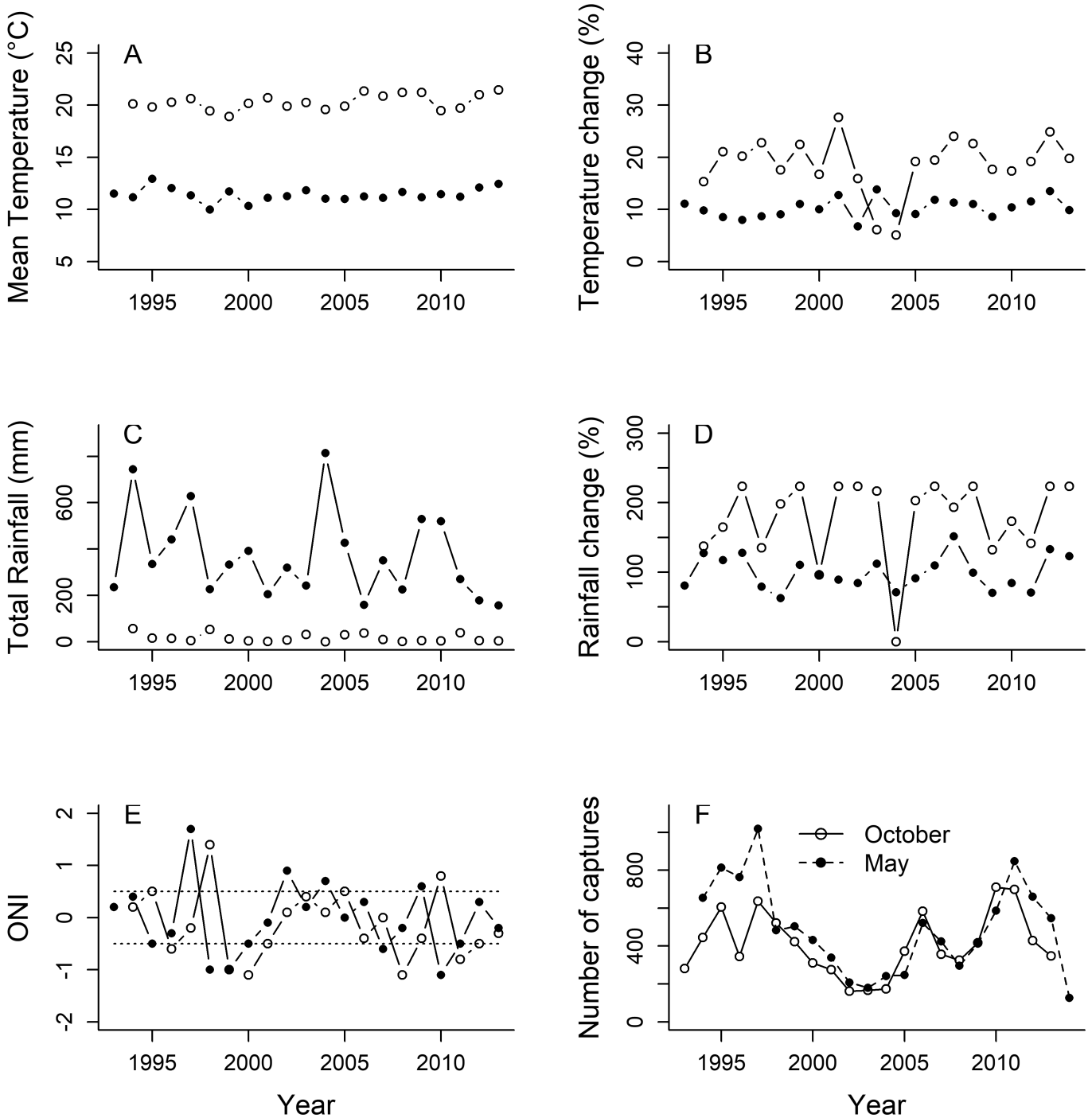
Fig. 2.—Annual fluctuations of climatic variables at Paso Robles (1993–2013) and number of captures of big-eared woodrats at Camp Roberts (1993–2014), California. Series were separated by season to highlight temporal variation between and within seasons. Black circles represent wet season (October–April) conditions or number of unique captures following a wet season, whereas white circles represent dry season (May–September) conditions or number of unique captures following a dry season. Mean temperatures are represented ± 1 *SE*. Rainfall level has three categories 1–3 for Low–High rain years. An Oceanic Niño Index (ONI) greater than 0.5 indicates a warm El Niño year, whereas ONI < -0.5 reflects a cooler La Niña year.

consecutive trapping sessions (i.e., just over 1 year), with a maximum of 12 seasons (i.e., 6 years). Overall, the sex-ratio was balanced (1:1).

Demographic parameters.—Ignoring the model with a time effect on all parameters (Φ, *p*, and *f*) because of a local convergence issue, the best general structure was time-dependent Φ, season-dependent *p*, and time-dependent *f* in the wet season (*f* in dry season fixed to 0; Table 1). Most annual survival parameters were not estimated in any of the time-dependent Φ models. However, even among models in

Table 1.—Model selection statistics testing for the effect of time (as a discrete variable) and season on the apparent survival probability (Φ), capture probability (*p*), and recruitment rate (*f*) of a big-eared woodrat (*Neotoma macrotis*) population in California between 1993 and 2014. For all models, *f* was fixed to 0 in the dry season; an effect of time on *f* therefore reflects annual variation in the wet season. Only the top 10 models are presented. The best model (italicized) has an AICc (Akaike Information Criterion corrected for small samples) weight of 1.00. *K* and np represent the number of estimated parameters and total number of parameters in a model, respectively; AICc is calculated using *K*. ΔAICc is the difference in AICc between a given model and the model with the lowest AICc. The AICc of the model with all parameters constant is 123,851.

Φ	*p*	*f*	*K*	np	AICc	ΔAICc
Time	*Season*	*Time*	*66*	*84*	*116,172.1*	*0*
Time	Constant	Time	66	83	116,300.7	128.6
Season	Time	Time	84	85	116,460.2	288.1
Constant	Time	Time	83	84	116,889.4	717.3
Season	Season	Time	45	45	117,651.7	1,479.6
Season	Constant	Time	43	44	117,831.4	1,659.3
Time	Time	Constant	77	84	118,042.4	1,870.3
Season	Time	Constant	45	45	118,042.5	1,871.4
Constant	Season	Time	43	44	118,157.4	1,985.3
Constant	Constant	Time	42	43	118,293.1	2,121.0

which Φ was not time-dependent, the best model still indicated time-dependent *p* and time-dependent *f* in the wet season, with a significant season effect on Φ (Table 1). Overall, *p* was 0.376 ± 0.004, but it was higher in the wet (0.404 ± 0.005) than in the dry season (0.344 ± 0.004). The overall monthly Φ was 0.945 ± 0.001; however, it was higher in the dry season (0.971 ± 0.001) than in the wet season (0.915 ± 0.001). The monthly recruitment rate (*f*) in the wet season was 0.064 ± 0.001 on average and ranged from 0.024 ± 0.004 (in 1998–1999) to 0.243 ± 0.043 (in 2004–2005). The monthly population growth rate (λ) varied from 0.996 ± 0.001 during the dry season to 1.001 ± 0.001 during the wet season. Despite high fluctuations in the number of unique captures and λ from year to year, the overall annual growth rate of 0.999 ± 0.001 indicates a stable rather than an increasing or decreasing population.

Effects of environmental covariates on vital rates.—Our analyses indicated that all climatic variables had a strong and significant effect on both Φ and *f*. The survival probability was positively influenced by *CV* of same-season rainfall, total past-season rainfall (i.e., with a one-season lag), same-season mean temperature (i.e., without a one-season lag), and *CV* of same-season temperature, but was negatively influenced by *CV* of past-season rainfall, total same-season rainfall, *CV* of past-season temperature, and past-season mean temperature (Table 2). All climatic effects on Φ were stronger in the dry than in the wet season, except for an equal effect of total same-season rainfall. The recruitment rate, in the wet season, was positively influenced by increasing *CV* of same-season rainfall, total past-season rainfall, *CV* of same-season temperature, and same-season mean temperature, whereas the effects of *CV* of past-season rainfall, total same-season rainfall, *CV* of past-season temperature, and past-season mean temperature were negative (Table 2).

The best model with a single weather variable included an interaction effect of season and same-season mean temperature on Φ, and an effect of same-season mean temperature on *f* (Table 3). The slope parameter for this climatic variable also was the largest, indicating that same-season mean temperature

had the strongest effect on Φ and *f*, although its effect on *f* was similar in magnitude to the effect of same-season rainfall (Table 2). Our best model indicated that, in the wet season, both Φ and *f* increased with same-season mean temperature; in the dry season, Φ also benefited from an increase in same-season mean temperature (Table 2; Fig. 3).

Consequently, the population growth rate increased with same-season mean temperature (Fig. 3). In the dry season, λ was close to 1 regardless of temperature conditions. In the wet season, λ increased with same-season mean temperature. However, the estimates of population growth rate derived from models with time-dependent Φ and *f* suggest that the relationship may be quadratic rather than linear, with a peak in λ between 11°C and 12°C (Fig. 3).

DISCUSSION

The visible and predicted impacts of climate change (Thorne et al. 2018) put small mammal species at risk of population declines and local extinctions. However, with recruitment and survival estimates remaining high under increased same-season temperature, low rainfall, and climatic variability, our study supports resilience to environmental changes occurring within the range of the big-eared woodrat, an inhabitant of woodlands in southern coastal central California. We discuss how its body size, life history strategy, diet, and house may contribute to its resilience, but that wildfires could become a serious threat to the persistence of some of its populations.

Positive effect of same-season mean temperature.—Contrary to our predictions, although rainfall was associated with changes in vital rates, temperature was surprisingly the most important factor for big-eared woodrat population dynamics. Specifically, same-season mean temperature had a positive effect both on survival and recruitment. This effect during the wet season was not surprising. The wet season also is the cooler season and a higher temperature probably helps with thermoregulation; metabolizing food high in toxic secondary plant compounds otherwise is necessary to produce body heat (Dearing et al. 2008). However, the same positive effect

Table 2.—Effect of climatic covariates on the apparent survival probability (Φ) and recruitment rate (*f*) of a big-eared woodrat population in California between 1993 and 2014. For each demographic parameter, beta estimates (with 95% confidence interval) are given based on the most parsimonious single-covariate model that included a given covariate (regardless of model structure for the other parameter). Beta estimates for the season are differences in survival or recruitment estimates between seasons, with the wet season as the reference; a positive difference indicates that the parameter was higher in the dry than in the wet season, whereas a negative difference indicates that the parameter was lower in the dry than in the wet season. Beta estimates for the covariate are slope estimates. Beta estimates for the interaction term correspond to the interaction between season and the indicated covariate, i.e., a difference in slope between seasons, with the wet season as the reference. Confidence intervals that do not include 0 indicate a significant effect. Capture probability was modeled as time-dependent. Highest rainfall and temperature slopes are bolded and estimates from the best model are italicized.

Covariate	Survival			Recruitment
	Season	Covariate	Interaction	Covariate
Rain_cv	1.951 (1.791; 2.110)	0.269 (0.195; 0.344)	0.989 (0.840; 1.138)	**0.729 (0.681; 0.777)**
Rain_cv_onelag	1.763 (1.572; 1.954)	−0.081 (−0.148; −0.014)	−0.799 (−0.922; −0.675)	−0.517 (−0.558; −0.475)
Rain_sum	1.433 (1.266; 1.599)	−0.479 (−0.544; −0.414)	−0.467 (−0.560; −0.374)	−0.554 (−0.597; −0.512)
Rain_sum_onelag	*2.832 (2.449; 1.599)*	***0.566 (0.425; 0.708)***	*2.893 (2.454; 3.332)*	0.599 (0.561; 0.638)
Temp_cv	1.720 (1.554; 1.886)	0.525 (0.433; 0.617)	1.067 (0.912; 1.222)	0.371 (0.338; 0.405)
Temp_cv_onelag	1.881 (1.692; 2.071)	−0.304 (−0.367; −0.240)	−1.028 (−1.153; −0.903)	−0.627 (−0.668; −0.585)
Temp_avg	*1.816 (1.543; 2.089)*	***0.742 (0.635; 0.849)***	*1.384 (1.148; 1.620)*	***0.701 (0.661; 0.740)***
Temp_avg_onelag	1.475 (1.281; 1.669)	−0.588 (−0.681; −0.495)	−0.974 (−1.123; −0.825)	−0.650 (−0.690; −0.610)

Table 3.—Model selection statistics testing for the effect of climatic variables on apparent survival probability (Φ) and recruitment rate (*f*) of a big-eared woodrat population in California between 1993 and 2014. Capture probability was time-dependent and *f* in the dry season (May–September) was fixed to 0 for all models. The symbol "+" indicates additive effect, whereas "*" represents both interaction and additive effects, respectively. *K* represents the number of parameters in a model; all parameters were estimated for all models. ΔAICc is the difference in AICc between a given model and the model with the lowest AICc, respectively. The top model has an AIC weight of 1. The reference model (Φ$_{season}$, p_{time}, $f_{constant}$) had AICc = 118,043.

Φ	*f*	*K*	AICc	ΔAICc
Season * Temp_avg	Temp_avg	48	116,675.5	0.0
Season + Temp_avg	Temp_avg	47	116,833.6	158.0
Season * Temp_avg	Temp_avg_onelag	48	116,907.0	231.4
Season * Rain_sum_onelag	Temp_avg	48	116,919.1	243.6
Season * Temp_avg_onelag	Temp_avg	48	116,927.4	251.9
Season + Rain_sum_onelag	Temp_avg	47	116,995.7	320.2
Season * Temp_cv	Temp_cv_onelag	48	117,006.2	330.7
Season + Temp_avg	Rain_sum_onelag	48	117,062.4	386.8
Season * Temp_cv_onelag	Temp_avg	48	117,062.5	387.0
Season * Rain_Sum	Rain_sum_onelag	48	117,068.8	393.2

of same-season mean temperature on survival during the dry season was surprising. In fact, higher temperatures decreased survival in two *Peromyscus* species at our study site (Tietje et al. 2018; Srivathsa et al. 2019). Results from other studies that have tested for an effect of temperature often have varied in direction and magnitude (Goswami et al. 2011; Greenville et al. 2012; Troyer et al. 2014), but the mechanism to explain this effect on the big-eared woodrat is unclear.

Like other woodrats, this species builds houses that protect them from temperature extremes (Lee 1963; Cameron and Rainey 1972). During the daytime, this nocturnal species remains in its house, which provides a moderate microclimate. In the summer, the temperature inside stick houses of desert (*N. lepida*) and dusky-footed woodrats can be 1–10°C below ambient temperature, and the relative humidity can be up to 28% higher than ambient air humidity (Lee 1963; Whitford and Steinberger 2010). The higher relative humidity minimizes evaporative water loss, thus increasing woodrat survival in the dry season (Cameron and Rainey 1972).

In addition, overall survival was lower for dusky-footed woodrats than for big-eared woodrats at their zone of contact just north of the study site (Fig. 1; Hunter et al. 2017). Big-eared woodrats, which are smaller than dusky-footed woodrats, may be better adapted to tolerate warmer temperatures. Although smaller than dusky-footed woodrats, Hunter et al. (2017) indicated that big-eared woodrats were the superior competitor, at least during the dry conditions that predominated during their study, which climate change models predict will prevail (Thorne et al. 2018).

Contrasting effects of same- and past-season rainfall.— Despite a general, positive effect on the vital rates of small mammals on the study area (Tietje et al. 2018; Srivathsa et al. 2019) and elsewhere (Madsen and Shine 1999; Klinger 2007), rainfall can have contrasting effects (Kneip et al. 2011; Cordes et al. 2020). Contrary to our prediction, big-eared woodrat survival and recruitment did not increase with same-season rainfall. Woodrat houses afford protection from predators and provide a place to store food. However, heavy rain can damage
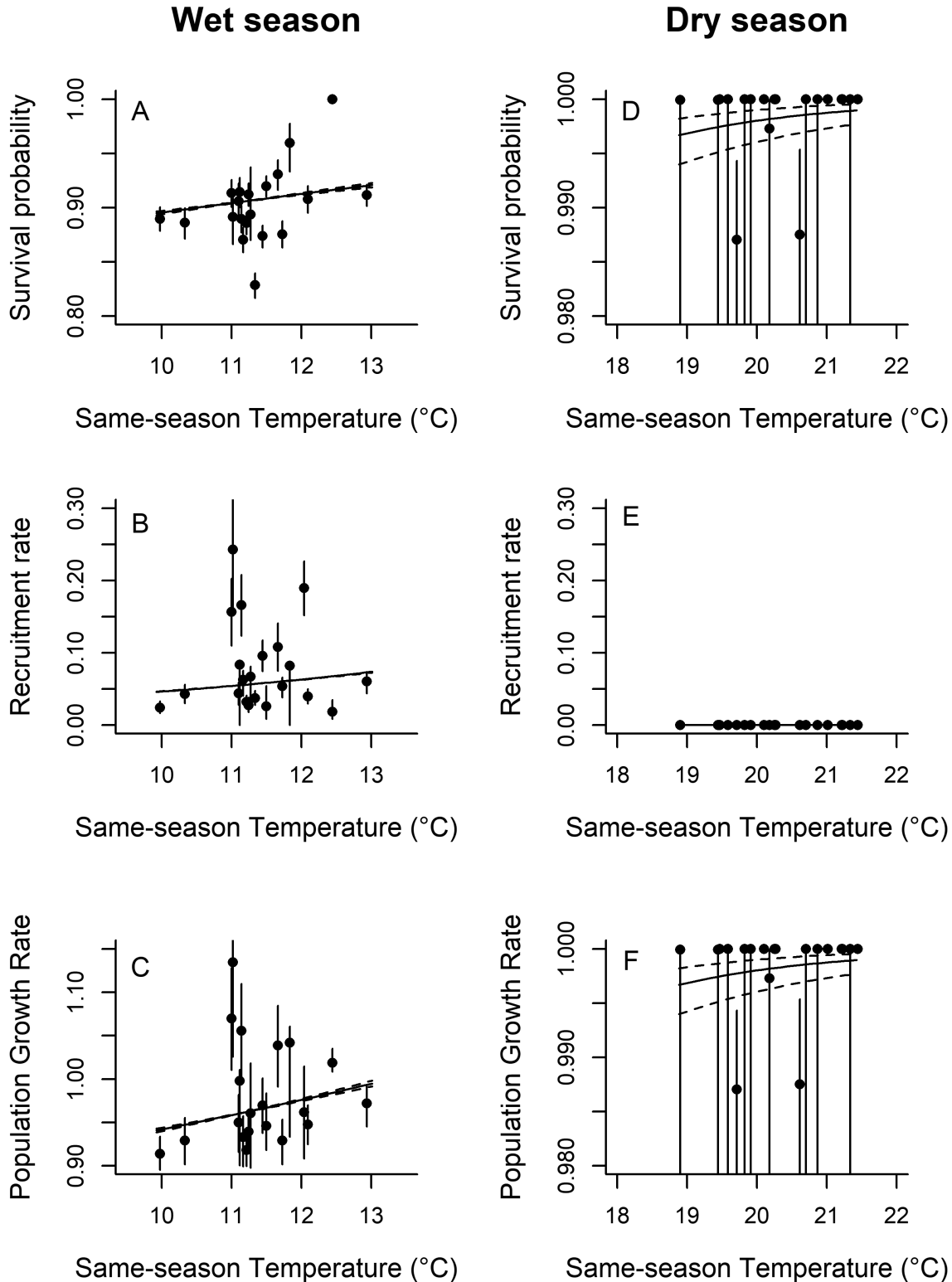
Fig. 3.—Effects of mean temperature in the wet (left; A–C) and dry (right; D–F) seasons on monthly survival probability (top; A, D), monthly recruitment rate (middle; B, E), and monthly realized population growth rate (bottom; D, F) of the big-eared woodrat at Camp Roberts, California. Points (with error bars as 95% confidence intervals) are estimates from time-dependent models, whereas lines (with 95% confidence intervals) are estimates from the best single-covariate model, which included an interaction effect of season and same-season mean temperature on survival, and an effect of same-season mean temperature on recruitment. Note that in the dry season recruitment was fixed to 0 (E) and population growth rate was therefore equal to survival.

houses and spoil food storage (Vestal 1938), which could explain why survival and recruitment decreased as same-season rainfall increased. Hunter et al. (2017) obtained similar results at a site just north of ours (Fig. 1) and suggested that periods of heavy rainfall may also favor parasites (Furman 1968; Stones and Hayward 1968) and diseases (Stapp et al. 2004). In addition to water, increased temperature accelerates food spoilage both by bacteria and fungi (McMeekin et al. 1987; Parra and Magan 2004). Higher temperature and precipitation also can increase survival and subsequent growth or spread of plant pathogens (Velásquez et al. 2018). Therefore, food spoilage and plant pathogens could further explain the lowered survival when warm temperatures and wetter conditions co-occur during the wet season.

Nonetheless, survival fluctuated positively with past-season rainfall, possibly because the amount of rainfall during the past year can affect coast live oak acorn production (Koenig et al. 1996), which may influence woodrat survival (Hunter et al. 2017). Coffeeberry is sensitive to water stress (Davis and Mooney 1986), which may have affected the quality and abundance of its leaves. Similarly, the nutritional quality of coast live oak leaves declines during droughts (Callaway and Nadkarni 1991), which, in some other mammals, can reduce lactation quality and force a switch in their diet (Lashley and Harper 2012).

More surprisingly yet, big-eared woodrats at our site had a higher survival rate during the hot, dry season than in the cool, wet season. This result and the similar body mass (an index of body condition; see Supplementary Data SD1) in the wet and dry seasons may be attributed to stable year-round foods of the big-eared woodrat, such as coffeeberry and coast live oak leaves (Vestal 1938; Atsatt and Ingram 1983). The big-eared woodrat may also be capable of adjusting its diet to locally available foods, as demonstrated by the closely related dusky-footed woodrat (McEachern et al. 2006). Overall, we expected that survival and body mass would suffer under conditions of variable rainfall, but they did not. Other factors are probably involved in big-eared woodrat survival but remain to be determined, and with changing environmental conditions, further study is warranted.

Seasonal variability in vital rates: a trade-off for a slow life history strategy?.—The life history strategies of mammals have been ranked on a slow–fast continuum (Gaillard et al. 1989; Oli 2004) with much variation in reproductive strategies even within a family (Dobson and Oli 2008). The continuum reflects opposite trade-offs between somatic and reproductive effort (Stearns 1992); species with a slow life history strategy tend to produce fewer offspring and live longer than species with a fast life history strategy. Relative to the other Cricetidae in the small mammal community on the study area, big-eared woodrats have a low monthly recruitment rate of 0.064, which contrasts with 0.146 for the California mouse (*Peromyscus californicus*—Tietje et al. 2018) and 0.18 for the piñon mouse (*P. truei*—Srivathsa et al. 2019). Moreover, its average litter size is 2.6 (Carraway and Verts 1991) compared with 4–8 for most rodent species (Gilbert 1986). Finally, during the hot, dry

season, survival remained high and recruitment was negligible, suggesting that big-eared woodrats may skip reproduction to favor survival over recruitment during the dry season, with this trade-off switching during the wet season when survival is lower and recruitment is higher. Therefore, the big-eared woodrat, which we can characterize as a slow species relative to other species in the same family, would be better adapted to climate change, at least in the short term (Isaac 2009). Although its long-term future may be challenged as increasing temperatures exceed its thermal tolerance, the species may be able to adapt by reducing its body size—an adaptation that occurred in other woodrats at a higher pace in the late Quaternary than needed during current climate change (Smith and Betancourt 2006); by switching to a more semelparous strategy—another late Quaternary adaption used by the desert woodrat (Smith and Charnov 2001); or by moving northward—a pattern currently observed within the hybrid zone between big-eared and dusky-footed woodrats (Hunter et al. 2017).

A more concerning and current threat is the increase in frequency and intensity of wildfires. Woodrat houses are highly flammable. On our study site, a low-intensity prescribed fire resulted in a third of woodrat houses burned (Vreeland and Tietje 2002) and fewer juveniles per adult female the following spring (Lee and Tietje 2005). Although this low-intensity fire did not reduce woodrat abundance (Vreeland and Tietje 2002), large wildfires can severely decrease big-eared woodrat populations due to the loss of necessary cover and food resources (Brehme et al. 2011). Thus, despite coast live oak's high resistance to fire (Thorne et al. 2016), the projected higher frequency of large wildfires (Barbero et al. 2015) may threaten the persistence of big-eared woodrats.

Implications, limitations, and conclusions.—Our results have important ecological implications because big-eared woodrats are ecological engineers that provide, via their stick houses, food and shelter to a suite of other vertebrate and invertebrate commensal species (Carraway and Verts 1991; Whitford and Steinberger 2010). However, one caveat is that we were unable to assess the predictive power of our models because of local convergence issues with time-dependent models. In addition, although the climatic variables we tested all had significant effects on survival and recruitment in our big-eared woodrat population, there may have been compensatory or synergistic effects among some of these variables. Other factors such as age at maturity (Oli and Dobson 1999) and population density (Kelt et al. 2019) can influence small mammal population demography. Last, responses to climatic variables can be nonlinear (Brown and Ernest 2002; Stenseth and Mysterud 2002; Goswami et al. 2011) and density-driven factors (e.g., competition, predation, and diseases) can modify the response of population growth rate to precipitation (Brown and Ernest 2002; Lima et al. 2008; Goswami et al. 2011).

Future climate change projections for the Southwest United States (Garfin et al. 2013) predict warmer temperatures and more erratic weather, more frequent and prolonged droughts (Smith et al. 2015), and more frequent large wildfires. Our results indicate that the big-eared woodrat population on our

study site in coastal central California survived well under climatic conditions experienced over 21 years of study. Its tolerance for warm temperature along with the house microclimate, stable food supply, and slow life history strategy (relative to other cricetids in the community) may all contribute to reduce its vulnerability to climate change. Therefore, our results add empirical support to the predictions of several authors that big-eared woodrats may be adequately equipped to cope with impending climate warming (Cameron and Rainey 1972; Hunter et al. 2017). Nonetheless, increasingly frequent large wildfires may threaten some populations.

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SUPPLEMENTARY DATA

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

Supplementary Data SD1.—Seasonal fluctuations in woodrat body mass.

LITERATURE CITED

ABDI, H. 2007. Z-scores. Pp. 1057–1058 in Encyclopedia of measurement and statistics (N. Salkind, ed.). Sage Publishing. Thousand Oaks, California.

ARMITAGE, K. B. 2013. Climate change and the conservation of marmots. Natural Science 5:36–43.

ATSATT, P. R., AND T. INGRAM. 1983. Adaptation to oak and other fibrous, phenolic-rich foliage by a small mammal, *Neotoma fuscipes*. Oecologia 60:135–142.

BARBERO, R., J. T. ABATZOGLOU, N. K. LARKIN, C. A. KOLDEN, AND B. STOCKS. 2015. Climate change presents increased potential for very large fires in the contiguous United States. International Journal of Wildland Fire 24:892–899.

BRADLEY, R. D., ET AL. 2006. Rapid recovery of rodent populations following severe drought. Southwestern Naturalist 51:87–93.

BREHME, C. S., D. R. CLARK, C. J. ROCHESTER, AND R. N. FISHER. 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. Fire Ecology 7:81–98.

BROWN, J. H., AND S. K. M. ERNST. 2002. Rain and rodents: complex dynamics of desert consumers. BioScience 52:979–987.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag. New York.

CALLAWAY, R. M., AND N. M. NADKARNI. 1991. Seasonal patterns of nutrient deposition in a *Quercus douglasii* woodland in central California. Plant and Soil 137:209–222.

CAMERON, G. N., AND D. G. RAINEY. 1972. Habitat utilization by *Neotoma lepida* in the Mohave Desert. Journal of Mammalogy 53:251–266.

CARRAWAY, L. N., AND B. J. VERTS. 1991. *Neotoma fuscipes*. Mammalian Species 186:1–10.

CHESSON, P., ET AL. 2004. Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. Oecologia 141:236–253.

CORDES, L. S., ET AL. 2020. Contrasting effects of climate change on seasonal survival of a hibernating mammal. Proceedings of the National Academy of Sciences of the United States of America 117:18119–18126.

DAVIS, S. D., AND H. A. MOONEY. 1986. Water use patterns of four co-occurring chaparral shrubs. Oecologia 70:172–177.

DEARING, M. D., J. S. FORBEY, J. D. MCLISTER, AND L. SANTOS. 2008. Ambient temperature influences diet selection and physiology of an herbivorous mammal, *Neotoma albigula*. Physiological and Biochemical Zoology 81:891–897.

DIAL, K. P. 1988. Three sympatric species of *Neotoma*: dietary specialization and coexistence. Oecologia 76:531–537.

DOBSON, F. S., AND M. K. OLI. 2008. The life histories of orders of mammals: fast and slow breeding. Current Science 95:862–865.

ELIAS, S. P., J. W. WITHAN, AND M. L. HUNTER. 2004. *Peromyscus leucopus* abundance and acorn mast: population fluctuation patterns over 20 years. Journal of Mammalogy 85:743–747.

ENGLISH, P. F. 1923. The dusky-footed wood rat (*Neotoma fuscipes*). Journal of Mammalogy 4:1–9.

FELDHAMER, G. A., AND A. K. POOLE. 2008. Status and conservation of other at-risk species of North American woodrats. Pp. 193–206 in The Allegheny woodrat (J. D. Peeles and J. Wright, eds.). Springer. New York.

FURMAN, D. P. 1968. Effects of the microclimate on parasitic nest mites of the dusky footed wood rat, *Neotoma fuscipes* Baird. Journal of Medical Entomology 5:160–168.

GAILLARD, J.-M., D. PONTIER, D. ALLAINÉ, J. D. LEBRETON, J. TROUVILLIEZ, AND J. CLOBERT. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56:59–76.

GARFIN, G., A. JARDINE, R. MERIDETH, M. BLACK, AND S. LEROY. 2013. Assessment of climate change in the southwest United States: a report prepared for the National Climate Assessment. Island Press. Washington, D.C.

GILBERT, A. N. 1986. Mammary number and litter size in Rodentia: the "one-half rule". Proceedings of the National Academy of Sciences of the United States of America 83:4828–4830.

GILLESPIE, S. C., D. H. VAN VUREN, D. A. KELT, J. M. EADIE, AND D. W. ANDERSON. 2008. Dynamics of rodent populations in semiarid habitats in Lassen County, California. Western North American Naturalist 68:76–82.

GOSWAMI, V. R., L. L. GETZ, J. A. HOSTETLER, A. OZGUL, AND M. K. OLI. 2011. Synergistic influences of phase, density, and climatic variation on the dynamics of fluctuating populations. Ecology 92:1680–1690.

GREENVILLE, A. C., G. M. WARDLE, AND C. R. DICKMAN. 2012. Extreme climatic events drive mammal irruptions: regression

analysis of 100-year trends in desert rainfall and temperature. Ecology and Evolution 2:2645–2658.

HALEY, S. L., J. G. LAMB, M. R. FRANKLIN, J. E. CONSTANCE, AND M. D. DEARING. 2007a. Xenobiotic metabolism of plant secondary compounds in juniper (*Juniperus monosperma*) by specialist and generalist woodrat herbivores, genus *Neotoma*. Comparative Biochemistry and Physiology, C. Toxicology & Pharmacology 146:552–560.

HALEY, S. L., J. G. LAMB, M. R. FRANKLIN, J. E. CONSTANCE, AND M. D. DEARING. 2007b. Xenobiotic metabolism of plant secondary compounds in oak (*Quercus agrifolia*) by specialist and generalist woodrat herbivores, genus *Neotoma*. Journal of Chemical Ecology 33:2111–2122.

HUNTER, E. A., M. D. MATOCQ, P. J. MURPHY, AND K. T. SHOEMAKER. 2017. Differential effects of climate on survival rates drive hybrid zone movement. Current Biology 27:3898–3903.

IPCC [INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE]. 2018. Summary for policymakers. Pp. 1–24 in Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty (V. Masson-Delmotte et al., eds.). IPCC and World Meteorological Organization. Geneva, Switzerland.

ISAAC, J. 2009. Effects of climate change on life history: implications for extinction risk in mammals. Endangered Species Research 7:115–123.

JAKSIC, F. M. 2001. Ecological effects of El Niño in terrestrial ecosystems of western South America. Ecography 24:241–250.

KELLY, L. T., R. DAYMAN, D. G. NIMMO, M. F. CLARKE, AND A. F. BENNETT. 2013. Spatial and temporal drivers of small mammal distributions in a semi-arid environment: the role of rainfall, vegetation and life-history. Austral Ecology 38:786–797.

KELT, D. A., ET AL. 2019. Advances in population ecology and species interactions in mammals. Journal of Mammalogy 100:965–1007.

KLINGER, R. 2007. Catastrophes, disturbances and density-dependence: population dynamics of the spiny pocket mouse (*Heteromys desmarestianus*) in a neotropical lowland forest. Journal of Tropical Ecology 23:507–518.

KNEIP, E., D. H. VAN VUREN, J. A. HOSTETLER, AND M. K. OLI. 2011. Influence of population density and climate on the demography of subalpine golden-mantled ground squirrels. Journal of Mammalogy 92:367–377.

KOENIG, W. D., J. M. H. KNOPS, W. J. CARMEN, M. T. STANBACK, AND R. L. MUMME. 1996. Acorn production by oaks in central coastal California: influence of weather at three levels. Canadian Journal of Forest Research 26:1677–1683.

KURNATH, P., N. D. MERZ, AND M. D. DEARING. 2016. Ambient temperature influences tolerance to plant secondary compounds in a mammalian herbivore. Proceedings of the Royal Society of London, B: Biological Sciences 283:20152387.

LAAKE, J. L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center. Processed Rep. 2013-01. National Marine Fisheries Service. Seattle, Washington.

LASHLEY, M. A., AND C. A. HARPER. 2012. The effects of extreme drought on native forage nutritional quality and white-tailed deer diet selection. Southeastern Naturalist 11:699–710.

LEE, A. K. 1963. The adaptations to arid environments in wood rats of the genus *Neotoma*. University of California Publications in Zoology 64:57–96.

LEE, D. E., AND W. D. TIETJE. 2005. Dusky-footed woodrat demography and prescribed fire in a California oak woodland. Journal of Wildlife Management 69:1211–1220.

LIMA, M., S. K. ERNEST, J. H. BROWN, A. BELGRANO, AND N. C. STENSETH. 2008. Chihuahuan Desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. Ecology 89:2594–2603.

LINSDALE, J. M., AND L. P. TEVIS. 1951. The dusky-footed woodrat. University of California Press. Berkeley, California.

LINSDALE, J. M., AND L. P. TEVIS. 1956. A five-year change in an assemblage of wood rat houses. Journal of Mammalogy 37:371–374.

M'CLOSKEY, R. T. 1972. Temporal chances in populations and species diversity in a California rodent community. Journal of Mammalogy 53:657–676.

MADSEN, T., AND R. SHINE. 1999. Rainfall and rats: climatically-driven dynamics of a tropical rodent population. Australian Journal of Ecology 24:80–89.

MATOCQ, M. D. 2002. Morphological and molecular analysis of a contact zone in the *Neotoma fuscipes* species complex. Journal of Mammalogy 83:866–883.

MATOCQ, M. D. 2004. Reproductive success and effective population size in woodrats (*Neotoma macrotis*). Molecular Ecology 13:1635–1642.

MATOCQ, M. D., AND E. A. LACEY. 2004. Philopatry, kin clusters, and genetic relatedness in a population of woodrats (*Neotoma macrotis*). Behavioral Ecology 15:647–653.

MCEACHERN, M. B., C. A. EAGLES-SMITH, C. M. EFFERSON, AND D. H. VAN VUREN. 2006. Evidence for local specialization in a generalist mammalian herbivore, *Neotoma fuscipes*. Oikos 113:440–448.

MCMEEKIN, T. A., ET AL. 1987. A model for combined effect of temperature and salt concentration/water activity on the growth rate of *Staphylococcus sylosus*. Journal of Applied Bacteriology 62:453–550.

MORENO, J., AND A. P. MØLLER. 2011. Extreme climatic events in relation to global change and their impact on life histories. Current Zoology 57:375–389.

NICHOLS, J. D. 2016. And the first one now will later be last: time-reversal in Cormack-Jolly-Seber models. Statistical Science 31:175–190.

NULL, J. 2017. Misconceptions of El Niño and La Niña. http://ggweather.com/enso/enso_myths.htm. Accessed 30 November 2020.

OLI, M. K. 2004. The fast-slow continuum and mammalian life-history patterns: an empirical evaluation. Basic and Applied Ecology 5:449–463.

OLI, M. K., AND F. S. DOBSON. 1999. Population cycles in small mammals: the role of age at sexual maturity. Oikos 86:557–565.

PARRA, R., AND N. MAGAN. 2004. Modelling the effect of temperature and water activity on growth of *Aspergillus niger* strains and applications for food spoilage moulds. Journal of Applied Microbiology 97:429–438.

PRADEL, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 152:703–709.

R CORE TEAM. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. https://www.r-project.org/. Accessed 26 March 2021.

SCHEFFERS, B. R., ET AL. 2016. The broad footprint of climate change from genes to biomes to people. Science 354:719–730.

Schwinning, S., and O. E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141:211–220.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Smith, F. A. 1995. Den characteristics and survivorship of woodrats (*Neotoma lepida*) in the eastern Mojave Desert. Southwestern Naturalist 40:366–372.

Smith, F. A., and J. L. Betancourt. 2003. The effect of Holocene temperature fluctuations on the evolution and ecology of *Neotoma* (woodrats) in Idaho and northwestern Utah. Quaternary Research 59:160–171.

Smith, F. A., and J. L. Betancourt. 2006. Predicting woodrat (*Neotoma*) responses to anthropogenic warming from studies of the palaeomidden record. Journal of Biogeography 33:2061–2076.

Smith, F. A., and E. L. Charnov. 2001. Fitness trade-offs select for semelparous reproduction in an extreme environment. Evolutionary Ecology Research 3:595–602.

Smith, S. J., J. Edmonds, C. A. Hartin, A. Mundra, and K. Calvin. 2015. Near-term acceleration in the rate of temperature change. Nature Climate Change 5:333–336.

Spevak, T. A. 1983. Population changes in a Mediterranean scrub rodent assembly during drought. Southeastern Naturalist 28:47–52.

Srivathsa, A., W. Tietje, V. Rolland, A. Polyakov, and M. K. Oli. 2019. Climatic drivers of pinyon mouse *Peromyscus truei* population dynamics in a resource-restricted environment. Population Ecology 61:122–131.

Stapp, P., M. F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog metapopulations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment 2:235–240.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press. New York, New York.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. Proceedings of the Royal Society of London, B: Biological Sciences 99:13379–13381.

Stones, R. C., and C. L. Hayward. 1968. Natural history of the desert woodrat, *Neotoma lepida*. American Midland Naturalist 80:458–476.

Storlazzi, C. D., and G. B. Griggs. 2000. Influence of El Niño–Southern Oscillation (ENSO) events on the evolution of central California's shoreline. Geological Society of America Bulletin 112:236–249.

Thibault, K. M., S. K. M. Ernest, E. P. White, J. H. Brown, and R. Jacob. 2010. Long-term insights into the influence of precipitation on community dynamics in desert rodents. Journal of Mammalogy 91:787–797.

Thorne, J. H., R. M. Boynton, A. J. Holguin, J. A. E. Stewart, and J. Bjorkman. 2016. A climate change vulnerability assessment of California's terrestrial vegetation. California Department of Fish and Wildlife. Sacramento.

Thorne, J. H., J. Wraithwall, and G. Franco. 2018. California's changing climate 2018. California's fourth climate change assessment. Governor's Office of Planning and Research, State of California Energy Commission, and California Natural Resources Agency. Sacramento, California.

Tietje, W. D., A. Y. Polyakov, V. Rolland, J. E. Hines, and M. K. Oli. 2018. Climatic influences on demography of the California mouse (*Peromyscus californicus*) in semiarid oak woodland. Journal of Mammalogy 99:1149–1158.

Troyer, E. M., S. E. Cameron Devitt, M. E. Sunquist, V. R. Goswami, and M. K. Oli. 2014. Density dependence or climatic variation? Factors influencing survival, recruitment, and population growth rate of Virginia opossums. Journal of Mammalogy 95:421–430.

Velásquez, A. C., C. D. M. Castroverde, and S. Y. He. 2018. Plant-pathogen warfare under changing climate conditions. Current Biology 28:R619–R634.

Vestal, E. H. 1938. Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley Hills. Journal of Mammalogy 19:1–36.

Vreeland, J. K., and W. D. Tietje. 2002. Numerical response of small vertebrates to prescribed fire in California oak woodland. Pp. 91–99 in The role of fire in nongame wildlife management and community restoration: traditional uses and new directions; proceedings of a special workshop, Nashville, TN, 15 September 2000 (W. M. Ford, K. R. Russell, and C. E. Moorman, eds.). U.S. Forest Service, General Technical Report NE-288:1–152. USDA Forest Service, Northeastern Research Station. Newtown Square, Pennsylvania.

Weir, B. J. 1974. Reproductive characteristics of hystricognath rodents. Symposium of the Zoological Society of London 54:265–301.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Whitford, W. G., and Y. Steinberger. 2010. Pack rats (*Neotoma* spp.): keystone ecological engineers? Journal of Arid Environments 74:1450–1455.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press. San Diego, California.

Williams, D. F., J. Verner, H. F. Sakai, and J. R. Waters. 1992. General biology of major prey species of the California spotted owl. Pp. 207–210 in The California spotted owl: a technical assessment of its current status (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutiérez, G. I. Gould, Jr., and T. W. Beck, eds.). U.S. Forest Service, General Technical Report PSW-GTR-133. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California.