

## ORIGINAL ARTICLE

# Climatic drivers of pinyon mouse *Peromyscus truei* population dynamics in a resource-restricted environment

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## Abstract

Highly variable patterns in temperature and rainfall events can have pronounced consequences for small mammals in resource-restricted environments. Climatic factors can therefore play a crucial role in determining the fates of small mammal populations. We applied Pradel's temporal symmetry model to a 21-year capture–recapture dataset to study population dynamics of the pinyon mouse (*Peromyscus truei*) in a semi-arid mixed oak woodland in California, USA. We examined time-, season- and sex-specific variation in realized population growth rate ( $\lambda$ ) and its constituent vital rates, apparent survival and recruitment. We also tested the influence of climatic factors on these rates. Overall monthly apparent survival was  $0.81 \pm 0.004$  (estimate  $\pm$  SE). Survival was generally higher during wetter months (October–May) but varied over time. Monthly recruitment rate was  $0.18 \pm 0.01$ , ranging from  $0.07 \pm 0.01$  to  $0.63 \pm 0.07$ . Although population growth rate ( $\lambda$ ) was highly variable, overall monthly growth rate was close to 1.0, indicating a stable population during the study period ( $\lambda \pm SE = 0.99 \pm 0.01$ ). Average temperature and its variability negatively affected survival, whereas rainfall positively influenced survival and recruitment rates, and thus the population growth rate. Our results suggest that seasonal rainfall and variation in temperature at the local scale, rather than regional climatic patterns, more strongly affected vital rates in this population. Discerning such linkages between species' population dynamics and environmental variability are critical for understanding local and regional impacts of global climate change, and for gauging viability and resilience of populations in resource-restricted environments.

## KEYWORDS

apparent survival, capture-mark-recapture, climate change effects, realized population growth rate, recruitment, rodent demography

## 1 | INTRODUCTION

Understanding factors and processes that drive population dynamics and persistence has long been an important goal in ecology (Coulson et al., 2001; Krebs, 2013; Loeuille & Ghil, 2004). Many studies aiming to discern the relative roles of intrinsic (and other biotic interactions), and extrinsic climatic factors have shown that density-dependence and bioclimatic factors jointly determine population dynamics of many species (Coulson et al., 2001; Leirs et al., 1997; Previtali, Lima, Meserve, Kelt, & Gutiérrez, 2009; Solberg et al., 2001).

Nonetheless, the hypothesis that extrinsic environmental factors are the primary drivers of animal population dynamics, an idea championed by Andrewartha and Birch (1954), continues to receive empirical support, especially from studies conducted in unpredictable arid or semi-arid environments (Brown & Ernest, 2002; Dickman, Mahon, Masters, & Gibson, 1999; Lightfoot, Davidson, Parker, Hernández, & Laundré, 2012; Lima, Stenseth, Yoccoz, & Jaksic, 2001; Madsen & Shine, 1999).

In arid and semi-arid systems where water is a restricted resource, rainfall events facilitate pulses of increased

primary productivity (Huxman et al., 2004; Schwinning & Sala, 2004). Species adapted to such environments can respond rapidly to periodic increases in primary productivity, which can potentially lead to population outbreaks (Jaksic, 2001; Madsen & Shine, 1999). Prolonged drought, on the other hand, can adversely affect populations, sometimes leading to population collapses (e.g., Facka, Roemer, Mathis, Kam, & Geffen, 2010; Kelt, Wilson, & Konno, 2005). Climate change models predict that the frequency (and duration) of drought and heat waves will increase for most arid and semi-arid environments around the world (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010; IPCC, 2014; Knapp et al., 2008); climate change could therefore have more profound effects on species occupying such habitats. Discerning how species inhabiting arid or semi-arid environments respond to extrinsic factors such as rainfall and temperature is necessary to understand population-level responses to anthropogenic climate change.

Using a 21-year (1993–2014) capture-mark-recapture (CMR) dataset and Pradel's temporal symmetry model (Nichols, 2016; Pradel, 1996), we examined population ecology of the pinyon mouse (*Peromyscus truei*), a small nocturnal rodent inhabiting an oak (*Quercus* spp.) woodland in coastal-central California (Cassola, 2016). Our objectives were to: (a) provide estimates of survival, recruitment and realized population growth rates, (b) test for sex-specific, seasonal and temporal variation in the aforementioned parameters, and (c) quantify the influence of climatic variables on demographic parameters and realized population growth rate. We predicted rainfall would positively affect the vital rates, temperature would negatively affect the vital rates and that high variation in rainfall and temperature would negatively affect these rates. Depending on the species biology and the environment, survival and recruitment rates of some species are strongly influenced by large-scale climatic phenomena, such as North Atlantic Oscillation (e.g., black-legged kittiwake *Rissa tridactyla*: Frederiksen, Harris, Daunt, Rothery, & Wanless, 2004; Soay sheep *Ovis aries*: Coulson et al., 2001) or El Niño events (e.g., Darwin's finches *Geospiza* spp.: Grant & Grant, 1993). However, small mammals typically have restricted movement and are adapted to respond rapidly to small-scale changes in rainfall and temperature (Bradley et al., 2006; Madsen & Shine, 1999; Previtali et al., 2009; Southgate & Masters, 1996). Thus, we expected that pinyon mouse demographic parameters might be more strongly influenced by local rainfall and temperature, rather than by regional El Niño events.

## 2 | MATERIAL AND METHODS

### 2.1 | Study species

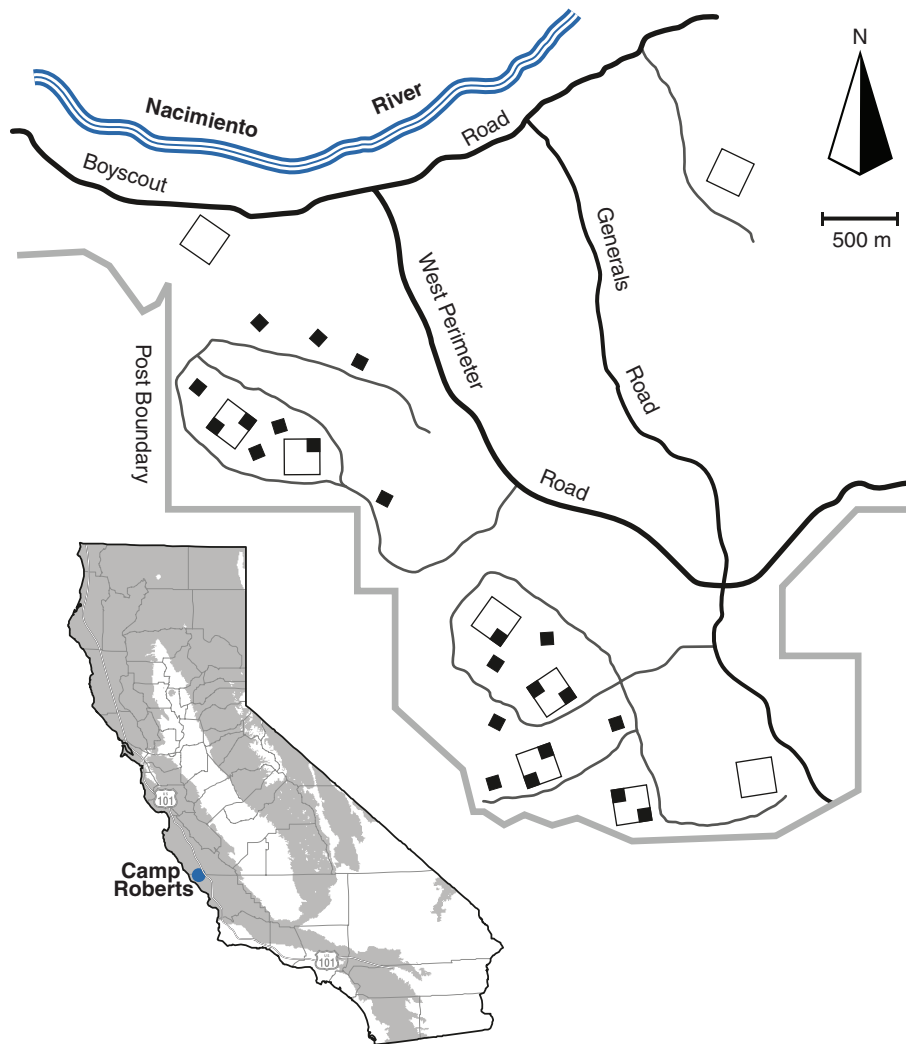
The pinyon mouse is a small nocturnal rodent, found in arid and semi-arid regions of central and western USA. It

is perhaps best adapted to the semi-arid pinyon-juniper woodlands that extend intermittently across most of Southwestern North America, from northern Mexico in the south to northwest US, along the Pacific Ocean. Within this broad area, five subspecies of *P. truei* are distributed within chaparral, desert scrub, redwood forests, riparian woodland and California oak woodland (Cassola, 2016; Hoffmeister, 1981; Rompola & Anderson, 2004). *P. truei gilberti* occupies our study area in coastal-central California (see study area description below). It prefers oak woodland habitat with dense tree cover, shrub understory and rocky outcrops (Rodhouse, Hirnyck, & Wright, 2010), generally nesting among rocks and sometimes in trees (Hall & Morrison, 1997). Although it breeds primarily in the dry season, breeding occurs through most of the year in Arizona and in some areas of Colorado, California and Nevada (Cassola, 2016; Hoffmeister, 1981). A polygynous mating system, large average litter size of 4 to 5 offspring and short time-to-maturity characterizes the life history attributes of the species (Ribble & Stanley, 1998). The average life span of the species is 1 to 2 years; our study therefore spanned  $\geq 10$  pinyon mouse generation times.

### 2.2 | Study area

We conducted our study at the National Guard Post Camp Roberts (hereafter, Camp Roberts), a 17, 000-ha military facility located in coastal-central California. Camp Roberts is located within an 8,000-ha matrix of grassland, chaparral and woodland called the “backcountry” (Figure 1). Climate in the study area is Mediterranean, with warm dry summers and cool-wet winters. Annual rainfall is highly variable and is influenced by El Niño/La Niña oscillations (Jong, Ting, & Seager, 2016). In this region, >95% of the rainfall occurs between October and April (henceforth, we refer to this wet season as “summer”). Very few rainfall events are observed between May and September (henceforth, we refer to this dry season as “winter”). The mean monthly rainfall during winter was 2.54 mm (range = 0 mm in July and 71.63 mm in June), compared to a monthly mean of 56.39 mm in summer (range = 0 mm in December and 312.67 mm in March).

The study area has pure stands of blue oak (*Quercus douglassii*), a mix of blue oak and coast live oak (*Quercus agrifolia*), typically with a shrub layer of up to 35% cover (Tietje et al., 2008), and a ground layer of introduced Mediterranean annual grasses (*Avena* spp.) and forbs, such as hummingbird sage (*Salvia spathacea*), wild peony (*Paeonia californica*) and miner's lettuce (*Claytonia perfoliata*). In the shrub layer, toyon (*Heteromeles arbutifolia*), red berry (*Rhamnus crocea*) and coffee berry (*Rhamnus californica*) are highest in the mesic sites, with proportionately more buck brush (*Ceanothus cuneatus*) and manzanita (*Arctostaphylos* spp.) on the more xeric



**FIGURE 1** Map of the study area. Trapping was carried out on nine 5.8-ha  $17 \times 17$  trapping grids (open, larger squares) from 1993 to 1996, and on twenty-two 1.1-ha  $8 \times 8$  trapping grids (solid, smaller squares) from 1997 to 2014. Inset map of California (adapted from California wildlife habitat relationships system range maps, California Department of Fish and Wildlife, California Interagency Wildlife Task Group, 2018). Location of the study area (solid circle) and the distribution of the Pinyon mouse (*Peromyscus truei*; grey shading) in California, USA

sites, where blue oak also predominates. In these blue oak stands, trees are larger and more widely spaced than in the mesic areas, where coast live oak predominates. Poison oak (*Toxicodendron diversilobum*) is found either as a solid blanket of vegetation, or scattered patches of individual stems (Tietje et al., 2008).

Although located in a military base, the study plots and surrounding areas were relatively undisturbed. Specifically, (a) the area was not used for military training; during around 1,000 daytime visits for field sampling, we did not observe any military personnel, (b) the only military-related activity was the annual grading of dirt roads, which provided access to our study area, (c) the last wild fire in the area occurred in 1953, and (d) other than the monitored hunting program during 1 weekend in late August and 1 week in November and December, Camp Roberts is closed to public access. There were no incidents of poisoning of rodents or other animals during our study.

### 2.3 | Field methods

In the winter of 1993, trained survey personnel laid nine 5.8-ha sampling plots in areas with  $>60\%$  tree canopy cover. Most study plots were on north- or east-facing slopes. During the summer of 1993, within each of the nine plots, we established a  $17 \times 17$  grid with 15-m spacing and marked the 289 intersections with a wood stake and survey flag with alphanumeric identifier. From 1993 to 2014, we trapped once during October and once during May. In the winter of 1996 to 1997, we increased the sample size by establishing twelve 1.1-ha plots, each with an  $8 \times 8$  grid with 15-m spacing. Starting in the winter of 1997, we sampled exclusively on twenty-two  $8 \times 8$  grids; i.e., on the 12 new sampling grids, plus on ten  $8 \times 8$  corners (either on one  $8 \times 8$  corner or two diagonal corners) on six of the 5.8-ha plots ( $17 \times 17$  grid) that we had sampled during 1993 to 1996 (see Figure 1).

We trapped small mammals once during October and once during May. During the winter and summer trapping sessions in 1993 to 1996, we trapped for five consecutive trap nights and after 1996, we trapped the 22 study plots for three consecutive nights. In each trapping session, we placed one Sherman live trap (3 × 3.5 × 30 cm; H.B. Sherman Traps, Inc., Tallahassee, FL) within 2 m of each grid intersection. To insulate trapped animals from overnight cold and from the heating of the interior of the trap by early morning sunshine, we placed traps in shade and covered them with litter from the vicinity of the trap. We baited traps with a mixture of rolled corn, oats, and barley laced with molasses. First captures were uniquely marked with a No. 100S-1 Monel ear tag (National Band and Tag Company, Newport, KY). For all captures, we recorded tag number, alphanumeric grid location, sex and age. Animals were released at the site of capture. Capture and handling of animals followed guidelines of the University of California, Berkeley, Institutional Animal Care and Use Committee (University of California, Berkeley (UCB), Permit #126A). Trapping also met the guidelines of the American Society of Mammalogists (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016).

## 2.4 | Analytical methods

Pradel's temporal symmetry model allowed us to decompose the population growth rate into its components, apparent survival and recruitment. Here, recruitment includes both new individuals added to the population through in situ reproduction, as well as immigration of individuals from outside the study area (Nichols, 2016; Nichols & Hines, 2002; Pradel, 1996). We used Pradel's model to estimate recapture probability ( $p$ ), apparent survival probability ( $\phi$ ), recruitment rate ( $f$ ) and realized population growth rate ( $\lambda$ ). First, we estimated  $\phi$ ,  $p$  and  $f$ , and tested for the additive and two-way interactive effects of sex (male or female), season (summer or winter), year (year of study), and time (across 41 seasons/42 trapping

occasions). We tested for seasonal and annual variation in  $\lambda$  similarly using the  $\phi$ - $\lambda$  parameterization of Pradel model. We then fitted a second set of models with singular climatic covariates (see the next section), allowing  $\phi$  and  $f$  to vary as a function of rainfall (with and without seasonal lag effects), temperature and El Niño index (see Table 1 for details). For the latter analyses, we allowed  $p$  to be affected by variable(s) from the four best-supported models (for  $p$ ) in the previous step.

In Pradel's model,  $\phi$  and  $f$  are modelled using the logit and log-link function, respectively. For example, writing  $\phi$  as a function of average temperature ( $temp\_avg$ ) and  $f$  as a function of the previous season's total rainfall ( $rain\_sum\_onelay$ ), we get

$$\phi = \frac{\exp(\beta_0 + \beta_1 \times temp\_avg)}{1 + \exp(\beta_0 + \beta_1 \times temp\_avg)}$$

$$f = \exp(\beta'_0 + \beta'_1 \times rain\_sum\_onelay).$$

Here  $\beta_0$  values are the intercept and  $\beta_1$  values are slope parameters, respectively. Because  $\lambda = \phi + f$ ,  $\lambda$  can be written in terms of these covariates as

$$\lambda = \frac{\exp(\beta_0 + \beta_1 \times temp\_avg)}{1 + \exp(\beta_0 + \beta_1 \times temp\_avg)} + \exp(\beta'_0 + \beta'_1 \times rain\_sum\_onelay).$$

We used these relationships to calculate  $\lambda$  as a function of climatic covariates affecting  $\phi$  and  $f$ . Exploratory analyses showed that most of the climatic covariates were highly correlated (Pearson correlation  $r > |0.6|$ ; Supporting Information Table S1), which is commonplace while dealing with climatic data (Graham, 2003; Grosbois et al., 2008). Analyses involving  $\geq 2$  correlated variables in the same model can lead to superfluous results. Consequently, we did not consider analyses using additive and/or interactive effects of multiple climatic variables.

## 2.5 | Covariates

High variability in rainfall can cause significant changes in plant production and community composition (Facka

**TABLE 1** Climatic covariates considered in modelling population vital rates (monthly apparent survival rate  $\phi$  and recruitment  $f$ ) for the pinyon mouse population in California, 1993 to 2014

Covariates	Description	$\phi$	$f$
<i>temp_avg</i>	Average seasonal temperature during season of capture	-0.31 (-0.35 to -0.27)*	0.12 (0.09 to 0.14)*
<i>temp_cv</i>	Seasonal variation (CV) in temperature the season of capture	-0.18 (-0.23 to -0.13)*	0.02 (-0.03 to 0.07)
<i>rain_sum</i>	Total seasonal rainfall during season of capture	0.13 (0.07 to 0.19)*	0.07 (0.02 to 0.13)*
<i>rain_sum_onelay</i>	Total seasonal rainfall during season before capture	-0.08 (-0.13 to 0.03)	0.21 (0.16 to 0.25)*
<i>rain_cv</i>	Seasonal variation (CV) in rainfall during season of capture	-0.15 (-0.20 to -0.11)*	0.13 (0.09 to 0.18)*
<i>rain_cv_onelay</i>	Seasonal variation (CV) in rainfall during season before capture	0.15 (0.09-0.19)*	-0.007 (-0.05 to 0.04)
<i>elnino</i>	Oceanic Niño Index (deflections from average tri-monthly sea surface temperature)	0.003 (-0.03 to 0.04)	0.09 (0.06 to 0.13)*

Note. Regression coefficients ( $\beta$  parameters) with 95% confidence intervals in parentheses are presented. Estimates with asterisk indicate that 95% confidence intervals do not straddle zero. The coefficients are based on the most parsimonious model that included a given covariate for each demographic rate. Because population growth rate  $\lambda = \phi + f$ , covariate effects on  $\lambda$  can be inferred based on their effects on  $\phi$  and  $f$ .

\*Indicate statistically significant results.

(CV), coefficient of variation.



et al., 2010; Huxman et al., 2004; Schwinning & Sala, 2004), which might affect food availability. It is also likely that highly variable temperature conditions reduce the ability of females to predict future conditions and therefore the environment in which their offspring will mature and reproduce (Monaghan, 2008). To evaluate these relationships, we tested for the effects on pinyon mouse population parameters of: (a) average seasonal temperature, (b) total seasonal precipitation; (c) coefficient of variation (CV) of average seasonal temperature and total seasonal precipitation, and (d) regional temperature anomalies (El Niño/La Niña oscillations). We used temperature and rainfall data recorded at the Paso Robles City weather station of the National Oceanographic and Atmospheric Agency (National Oceanographic and Atmospheric Administration (NOAA) 2016), located in Paso Robles, California, 11.7-km southeast of the study area. Seasonal averages and CVs of temperature and precipitation were computed from weekly data. Here, a season refers to summer or winter as explained in the study area description. In order to account for a plausible delay in the effect of rainfall via plant growth and primary production, we also included seasonal lag effects of these variables.

To test for the regional climatic effects, we used the Oceanic Niño Index to identify El Niño and La Niña events in the Pacific Ocean (see Lightfoot et al., 2012). El Niño or La Niña are characterized by consecutive 3-month sea surface temperatures, either above (El Niño) or below (La Niña) a threshold of  $\pm 0.5^\circ\text{C}$  from the average temperature measured above the equatorial Pacific Ocean. We obtained Oceanic Niño Index values from the NOAA National Weather Service Climate Prediction Center website ([www.cpc.noaa.gov/products/analysis\\_monitoring](http://www.cpc.noaa.gov/products/analysis_monitoring)). All the covariates were z-transformed prior to analysis so that model coefficients could be directly interpreted as effect sizes. The full list of covariates used in the analysis, their corresponding descriptions and their effects on survival and recruitment are in Table 1.

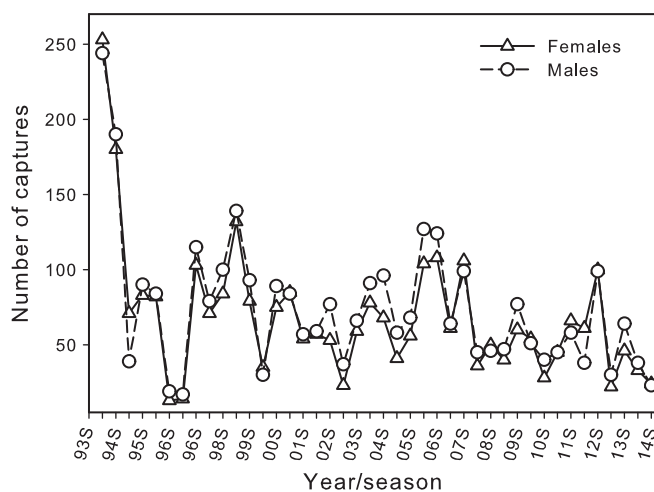
We relied on an information-theoretic approach for model selection (Burnham & Anderson, 2002; Williams, Nichols, & Conroy, 2002), with Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ) as a measure of model parsimony. The effect of environmental covariates was determined by comparing models with and without covariates, and by examination of 95% confidence intervals for the slope parameter ( $\beta$ ) defining the relationship between a demographic parameter and the covariates. We performed the analyses using the program MARK (White & Burnham, 1999) version 6.2 implemented using the RMark package (Laake, 2013) in program R (R Development Core Team, 2014). Although trapping occurred twice a year (May and October), we specified the time interval between successive samples in months in our CMR analyses; thus, all estimated parameters are monthly rates (or probabilities). Unless otherwise noted, mean or point estimate  $\pm SE$  is reported.

### 3 | RESULTS

#### 3.1 | Estimates of capture probability and demographic parameters

Our trapping effort (236,187 trap nights) yielded 6,029 captures of 4,596 unique individuals (average recaptures = 1.3 per mouse), with slightly more males captured compared to females (3,136 males and 2,893 females; Figure 2). The top-ranked model without climatic effects revealed that recapture probability was influenced by an interaction between sex and season (Table 2;  $\phi$ - $f$  parameterization). Recapture probability was higher for females than for males, and for both sexes, higher in winter (females:  $0.82 \pm 0.03$  [estimate  $\pm SE$ ]; males:  $0.77 \pm 0.03$ ) than in summer (females:  $0.81 \pm 0.03$ ; males:  $0.71 \pm 0.03$ ).

The overall monthly apparent survival probability ( $\phi$ ) was  $0.81 \pm 0.004$  (estimate  $\pm SE$  based on the top-ranked model from Table 2; see Supporting Information Table S2 for the full set of candidate models). Survival during summer was higher ( $0.84 \pm 0.003$ ) compared to winter ( $0.77 \pm 0.002$ ). Highest and lowest survival rates were recorded in the summer of 2005 ( $0.65 \pm 0.072$ ) and the winter of 1996 ( $0.91 \pm 0.010$ ) respectively (Figure 3a). The overall monthly recruitment rate ( $f$ ) during our study was estimated at  $0.18 \pm 0.01$  (estimate  $\pm SE$ ); recruitment rates did not differ between summer and winter. Seasonal recruitment rate was lowest in the summer of 1998 ( $0.07 \pm 0.011$ ) and peaked in the summer of 1996 ( $0.62 \pm 0.076$ , Figure 3b). The realized growth rate ( $\lambda$ ) indicated that the population was stable during our study period ( $\lambda = 0.99 \pm 0.001$ ; estimate  $\pm SE$ ), but  $\lambda$  varied substantially over time, ranging from  $0.77 \pm 0.02$  in the winter of 2012 to  $1.31 \pm 0.03$  in the summer of 1996 (Figure 3c). The population growth rate ( $\lambda$ ) was strongly correlated with recruitment (Pearson correlation  $r = 0.81$ ,  $p$  value  $< 0.005$ ),



**FIGURE 2** Number of captures of male and female pinyon mice in Camp Roberts, California. Captures correspond to 42 sessions, once in each summer and winter seasons, from 1993 to 2014. The first two numbers in x-axis label represent year of study, followed by season (S, spring)

**TABLE 2** Model comparison statistics testing for the effect of time, season and sex on survival ( $\phi$ ), capture probability ( $p$ ), growth rate ( $\lambda$ ) and recruitment ( $f$ ) of a pinyon mouse population using  $\phi$ - $f$  and  $\phi$ - $\lambda$  parameterization of Pradel model (Nichols, 2016; Williams et al., 2002)

Model	K	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	AIC <sub>c</sub> weight	Deviance
<i><math>\phi</math>-<math>f</math> parameterization</i>					
$\phi$ (time) $p$ (season $\times$ sex) $f$ (time)	86	39326.52	0	0.44	622.09
$\phi$ (time) $p$ (season + sex) $f$ (time)	85	39327.54	1.01	0.26	625.17
$\phi$ (time) $p$ (season) $f$ (time)	84	39328.57	2.04	0.16	628.25
$\phi$ (time + sex) $p$ (season + sex) $f$ (time)	86	39329.52	3.00	0.09	625.09
$\phi$ (time + sex) $p$ (season) $f$ (time + sex)	86	39332.14	5.61	0.02	627.71
<i><math>\phi</math>-<math>\lambda</math> parameterization</i>					
$\phi$ (time + sex) $p$ (season $\times$ sex) $\lambda$ (time)	87	39325.33	0	0.25	618.84
$\phi$ (time + sex) $p$ (season + sex) $\lambda$ (time)	86	39325.39	0.06	0.24	620.96
$\phi$ (time) $p$ (season $\times$ sex) $\lambda$ (time)	86	39326.52	1.19	0.14	622.09
$\phi$ (time + sex) $p$ (season + sex) $\lambda$ (time + sex)	88	39327.38	2.05	0.09	618.83
$\phi$ (time + sex) $p$ (season $\times$ sex) $\lambda$ (time + sex)	87	39327.42	2.09	0.09	620.93

Note. Top five candidate models (based on AIC<sub>c</sub> values) for  $\phi$ - $f$  and  $\phi$ - $\lambda$  parameterizations are shown. A "+" indicates additive effect and " $\times$ " indicates an interactive effect between predictor variables.

AIC<sub>c</sub>, Akaike information criterion corrected for small sample sizes; K, number of parameters.

while its correlation with apparent survival was weaker ( $r = 0.34$ ,  $p$  value  $< 0.001$ ).

### 3.2 | Effects of climatic variables

Analyses testing for singular effects of climatic covariates on demographic parameters revealed that (a) survival probability was positively influenced by total seasonal rainfall and CV of rainfall during the previous season, and negatively affected by average and CV of temperature, and CV of rainfall and (b) recruitment was positively influenced by total seasonal rainfall (with and without time lag), CV of rainfall, Oceanic Niño Index, and average temperature (Table 1; Supporting Information Table S3). The most parsimonious single variable model included a negative effect of average temperature on survival and a positive effect of total rainfall during the previous season on recruitment (Table S3; Figure 4). Because population growth rate in Pradel's model is the sum of survival and recruitment (Nichols, 2016), it follows that  $\lambda$  was negatively affected by average temperature and positively affected by the previous season's rainfall. Some climatic variables differentially affected  $f$  and  $\phi$ . For example, variability in rainfall negatively affected  $\phi$  but positively affected  $f$  (Table 1).

## 4 | DISCUSSION

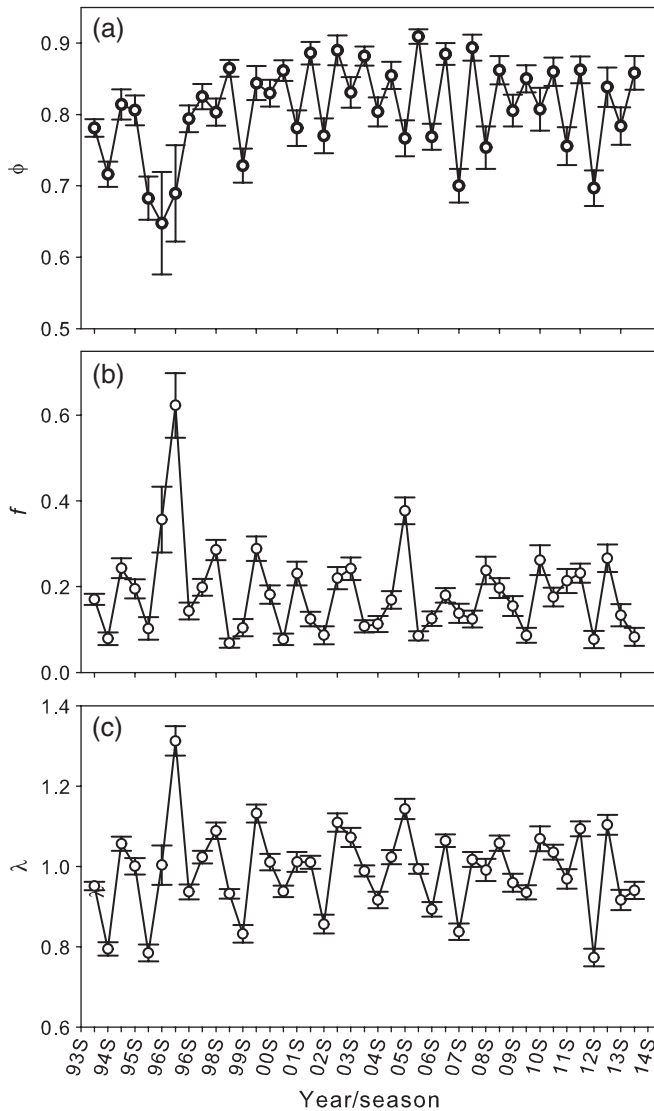
Although pinyon-juniper woodlands are widely distributed in the western United States, these habitats as well as their namesake inhabitant, the pinyon mouse, have received few scientific inquiries. Using 8 years of capture-mark-recapture data, Tietje et al. (2008) reported that the pinyon mouse population at Camp Roberts exhibited high temporal variation in abundance and survival. The present study augments the previous assessment, using the full 21-year data set to (a) provide for the first time, estimates of realized population growth rate, and its component demographic vital rates and

(b) test the effects of local and regional climatic variables on these demographic parameters.

### 4.1 | Recapture probabilities and demographic vital rates

Estimated recapture probability ( $p$ ) differed between sexes and varied between summer and winter. Females have much smaller home ranges than males and use a more restricted range of habitats (Ribble & Samson, 1987; Scheibe & O'Farrell, 1995). We found that females generally had higher recapture probabilities compared to males, probably because of higher site-fidelity (Scheibe & O'Farrell, 1995), while more mobile males are recaptured less frequently in our static traps. Estimates of recapture probabilities in our study (0.71–0.82) were much higher than those reported by Hammond & Anthony (2006) for pinyon mice from across their range ( $0.47 \pm 0.23$  [SE]).

Our study population was characterized by high seasonal survival rates (81%). High survival probabilities appear to be somewhat common in *Peromyscus* species; for example, Kendall, Nichols, and Hines (1997) found similar estimates (85%) for *Peromyscus leucopus*, and Crespin, Choquet, Lima, Merritt, and Pradel (2008) report much higher survival rates (93%) for *Peromyscus maniculatus*. Survival probabilities fluctuated seasonally, but were lower in 1994 and 1996. We suspect the decreased survival was a direct consequence of the major La Niña events in 1995 and 1996 with below-average winter precipitation. Most rainfall events in our study area are restricted to the months from October to April, with showers in March usually boosting the first flush, followed by a productivity pulse. The growth pulse during March–April plausibly sustains the population through the driest months of the following winter season. Recruitment rate peaked during the summer of 1996 ( $0.63 \pm 0.07$ ) and was lowest in the summer of 1998 ( $0.07 \pm 0.01$ ). Our



**FIGURE 3** Estimates of monthly (a) apparent survival rate  $\phi$ , (b) recruitment rates  $f$  and (c) realized population growth rate  $\lambda$  for the pinyon mouse population over 21 years, derived from the corresponding best-fit Pradel's temporal symmetry model. The first two numbers in x-axis label represent year of study, followed by season (S, winter)

preliminary analyses indicated that models with climatic covariates ranked an order of magnitude lower than models that included a time effect (based on  $AIC_c$  values), suggesting that the climatic variables we considered did not explain all of the temporal variability in recruitment.

Estimates of population growth rate differed between seasons, showing higher rates during summer than in winter (1.02 vs. 0.95). We also found that population growth rate was more strongly correlated with recruitment rates rather than survival probabilities ( $r = 0.81$  vs.  $r = 0.34$ ). Our results are consistent with documented relationships between life history strategies of mammals (fast/r-selected vs. slow/K-selected species) and their population vital rates, that is, growth rate is generally sensitive to survival in slow species and to recruitment in fast species (Oli, 2004; Oli & Dobson, 2003).

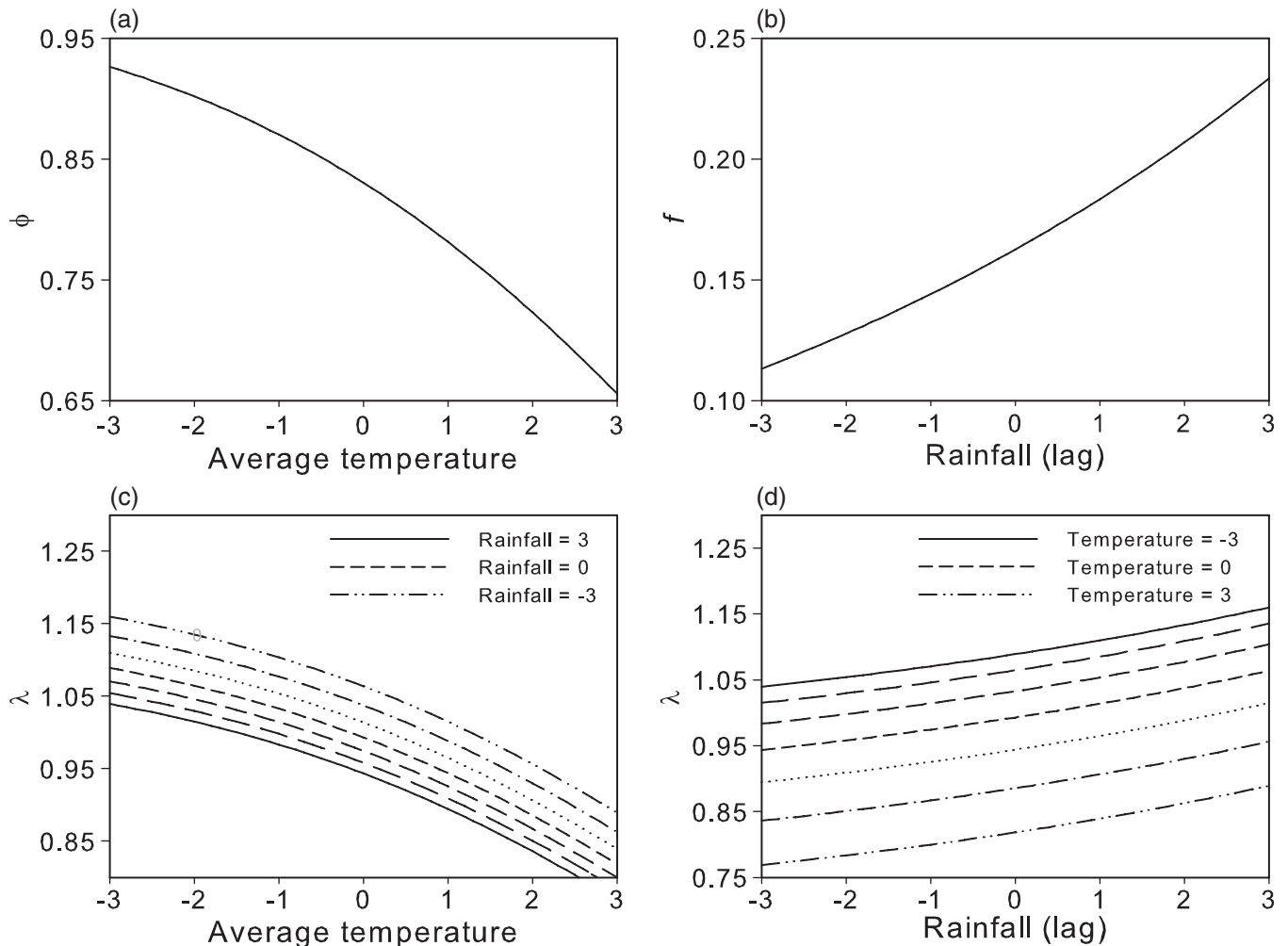
## 4.2 | Local and regional climatic effects on demographic rates

Seasonal rainfall positively influenced pinyon mouse survival and recruitment (and thus, population growth rate) in this semi-arid habitat. Previous seasons' rainfall events contributed to higher recruitment rates, most likely through rainfall's effect on vegetation and primary productivity. Corroborating our expectations, average seasonal temperature and fluctuations in seasonal temperature had negative effects on survival but not on recruitment rate. Consistent with the results from the singular covariate effects discussed above, we found that survival and recruitment (and thus, growth rate) remained low during hot-dry conditions, while population growth was generally favoured by cool-wet conditions. It appears therefore that rainfall-driven recruitment is vitally important for maintaining the growth rate in this population, particularly during periods of low survival.

Recent climate events have had notable impacts on spatial ecology of pinyon mice in Yosemite National Park, California, where Yang, Conroy, and Moritz (2011) show that climate change triggered elevation shifts and changes in their geographic distribution. Interestingly, we found that the influence of Oceanic Niño Index on the vital rates of pinyon mice was much weaker compared to local temperature and rainfall patterns (Table 1). The high recruitment rates, short time-to-maturity and short life span in pinyon mice perhaps make them relatively less sensitive to climate change. Given the overall stable nature of this population, the species may also show a certain level of resilience to some climatic extremes, as has been observed in other rodents in semi-arid habitats (Bradley et al., 2006; Brown, Whitham, Ernest, & Gehring, 2001). Taken together, we deduce that fluctuations in sea surface temperature (and other regional-scale climatic phenomena) may not directly alter population vital rates of pinyon mice, but their impacts are made visible through changes in local weather conditions (mainly, rainfall and temperature).

## 4.3 | Resource availability and ecological interactions

We identify two caveats in our study. First, we could not directly quantify the effect of food resources on the population vital rates. We relied instead on measures of precipitation, since rainfall patterns often serve as a reasonable surrogate of food availability in arid or semi-arid ecosystems (e.g., Letnic et al., 2011). We established that rainfall is an important factor influencing vital rates in this population of pinyon mice. In instances of extreme droughts, pinyon mice enter diurnal torpor, with a decline in urine concentration and an increase in faecal water content (Bradford, 1974), which likely enables their persistence. Second, predation is an important source of mortality for many small mammal populations (Andersson & Erlinge, 1977; Hanski, Henttonen, Korpimäki, Oksanen, & Turchin, 2001), and in some cases, can offset or mediate climatic effects (Greenville,



**FIGURE 4** Effects of climatic variables on survival, recruitment and growth rate. Average seasonal temperature and total rainfall from previous season ( $z$ -transformed) selected for apparent survival rate  $\phi$  (a) and recruitment rate  $f$  (b), respectively, based on the most parsimonious singular effect model (Table S3). Population growth rate  $\lambda$  (lower panel) was calculated as a derived parameter based on the effect of the relevant covariates on apparent survival  $\phi$  and recruitment  $f$  by noting that  $\lambda = \phi + f$ , and accounting for the appropriate link functions (logit link for  $\phi$ , and log link for  $f$ ). The most parsimonious model (Table S3) revealed that  $\phi$  was affected by temperature, and  $f$  by the previous season's rainfall; thus,  $\lambda$  was affected by both of these variables. Hence,  $\lambda$  is plotted as a function of: (c) average temperature ( $x$ -axis) for a range of values of previous season's rainfall (contours). The contour lines represent the relationship between  $\lambda$  and average temperature for total rainfall (one season time lag) ranging from  $-3$  (bottom contour) to  $3$  (top contour); (d) total rainfall (with one season time lag) ( $x$ -axis) for a range of average temperature ranging from  $-3$  (top contour) to  $3$  (bottom contour)

Wardle, & Dickman, 2017). But we lacked data on the distribution and abundance of mammalian or avian predators that may have influenced the pinyon mouse population changes. Nonetheless, our study provides the first comprehensive demographic analysis of pinyon mouse anywhere in its range, reports estimates of survival, recruitment and realized population growth rate using long-term data and statistically robust temporal symmetry model, and thus contributes substantially to our understanding of factors influencing pinyon mouse population dynamics.

## 5 | CONCLUSION

Several studies have predicted that an important consequence of global climate change would be hydrological

amplification, increased risk of drought, intense heat waves and higher frequency of rainfall events or flooding (Knapp et al., 2008). Such climatic changes could bear negative effects on many species, instigating local extinctions, geographic range shifts and altered population dynamics (Scheffers et al., 2016; Walther et al., 2002). Rainfall and temperature conditions are predicted to change throughout the range of the pinyon mouse. Temperature is predicted to increase over much of this specie's broad range by approximately 2 to 3°C by 2100, while average annual rainfall would decrease by 4 cm (Seager et al., 2007). In sum, the climate across the specie's range will become more variable. We are cautiously optimistic that this particular population may be reasonably resilient to current large-scale temperature fluctuations or sporadic events of extreme climates. While our study provides information from a relatively



undisturbed habitat, we recognize that these patterns would vary across space, time, fire regimes, intensities of anthropogenic disturbance or changes in the larger faunal community composition. Future studies will need to augment our findings by investigating how these dynamics and associated environmental factors differ between pinyon mouse populations in other regions and landscapes, across the species' geographic range.

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