Multiple coping strategies maintain stability of a small mammal population in resource-restricted environments

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Abstract - In semi-arid environments, aperiodic rainfall pulses determine cycles of plant production and resource availability for higher trophic levels, creating strong bottom-up regulation. The influence of climatic factors on population vital rates often shapes the dynamics of small mammal populations in such resource-restricted environments. Using a 21-year biannual capture–recapture dataset (1993 to 2014), we examined the impacts of climatic factors on the population dynamics of the brush mouse (*Peromyscus boylii*) in semi-arid oak woodland of coastal-central California. We applied Pradel's temporal symmetry model to estimate capture probability (p), apparent survival (φ), recruitment (f), and realized population growth rate (λ) of the brush mouse, and examined the effects of temperature, rainfall, and El Niño on these demographic parameters. The population was stable during the study period with a monthly realized population growth rate of $0.993 \pm$ SE 0.032, but growth varied over time from 0.680 ± 0.054 to 1.450 ± 0.083. Monthly survival estimates averaged 0.817 ± 0.005 and monthly recruitment estimates averaged 0.175 ± 0.038. Survival probability and realized population

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31 growth were positively correlated with rainfall and negatively correlated with temperature. In

32 contrast, recruitment was negatively correlated with rainfall and positively correlated with

33 temperature. Brush mice maintained their population through multiple coping strategies,

34 investing in high recruitment during warmer and drier periods and allocating more energy

35 towards survival during cooler and wetter conditions. Although climatic change in coastal-central

36 California will favor recruitment over survival, varying strategies may serve as a mechanism by

37 which brush mice maintain resilience in the face of climate change. Our results indicate that

38 rainfall and temperature are both important drivers of brush mouse population dynamics and will

39 play a significant role in predicting the future viability of brush mice under a changing climate.

40

41 *Introduction* - Changes in abundance of small mammal populations can result from

42 complex interactions among multiple factors, such as climate, plant production, food supply,

43 vegetative cover, predation, and competition (Oli and Dobson 2003). The debate over the relative

44 roles of endogenous (e.g., competition, predation) and exogenous (e.g., temperature, rainfall)

45 factors in population dynamics has resulted in a general agreement that both influence population

46 fluctuations (Turchin 2003). However, some studies in semi-arid systems show that exogenous

47 factors outweigh endogenous factors in driving small mammal population dynamics and are key

48 to understanding fluctuations (Gutierrez et al. 2010, Previtali et al. 2009), particularly for

49 evaluating the persistence of populations on the margins of a species' distribution (Gillespie et al.

50 2008).

51 Semi-arid landscapes are highly variable in seasonal and annual rainfall patterns,

52 typically with hot, dry summers and cool, wet winters. These systems are also resource-restricted,

53 exhibiting pulse-like patterns of annual rainfall (averaging 25–50 cm) and large seasonal

54   fluctuations, with nearly all rainfall occurring in the fall and winter months (Peel et al. 2007).

55   Fluctuations in rainfall may also be erratic, with some years of high and above-average

56   precipitation (due to the El Niño effect in some areas), and other years of very little precipitation,

57   leading to drought-like conditions (Previtali et al. 2009). In such systems, precipitation typically

58   drives plant productivity, primarily through seed production and foliage growth (Brown and

59   Ernest 2002, Heske et al. 1994, Meserve et al. 2003, Lima et al. 2002).

60   Many studies show that dramatic changes in precipitation have strong effects on

61   population dynamics of small mammals, with rainfall pulses driving rodent dynamics indirectly

62   through primary production, such as food availability and cover (Brown and Ernest 2002, Heske

63   et al. 1994, Knapp et al. 2008, Meserve et al. 2003, Yates et al. 2002). Conversely, drought can

64   have a detrimental effect on rodent population dynamics by reducing plant productivity (Brown

65   and Ernest 2002, Meserve et al 2003), sometimes leading to population collapse (Facka et al.

66   2010). However, we know relatively little about the effect of temperature on small mammal

67   population dynamics in semi-arid climates, although some studies suggest that the effects of

68   temperature are seasonal, showing a negative correlation with survival and recruitment in

69   summer and a positive correlation in winter (Myers et al. 1985, Luis et al. 2010).

70   Due to their short life cycles, small mammals serve as ideal study systems for long-term,

71   multi-generational studies. Short life spans and fast reproduction also translate to quick responses

72   to changes in climatic conditions (Previtali et al. 2009). The brush mouse *Peromyscus boylii* has

73   a wide distribution in the United States, occurring throughout much of the southwest and most of

74   California, except for major grassland and desert areas (Baker 1968). This species is typically

75   found in mature chaparral, oak woodland and hardwood conifer communities (Baker 1968). As

76   its name suggests, the brush mouse prefers significant amounts of tree cover, dense and shrubby

77   vegetation, rock cover, and logs, which are important habitat structures that provide shelter from

78   weather and predators, as well as nesting sites (Bradley and Schmidly 1999, Brehme et al. 2011,

79   Gottesman et al. 2004). The brush mouse plays an important role in ecosystem function as a key

80   prey species for the federally threatened Mexican spotted owl, *Strix occidentalis lucida* (Boyett

81   2001). In the southwestern United States, the brush mouse is also a reservoir host for hantavirus

82   (Abbott et al. 1999), making studies of population dynamics important for predicting rates of

83   disease prevalence and spread. Anthropogenic impacts on brush mouse habitat include exurban

84   development and increasing wildfire intensity (Brehme et al. 2011). From our knowledge, no

85   study has yet provided estimates of apparent survival, recruitment, and realized population

86   growth rate of the brush mouse, essential for understanding population dynamics of this species.

87   Our goal was to examine the effects of temperature, precipitation and El Niño on the

88   population dynamics of the brush mouse in a coastal-central California mixed-oak-woodland. We

89   applied temporal symmetry capture-mark-recapture (CMR) models (Pradel 1996; Nichols et al.

90   2000; Williams et al. 2002) to a long-term (1993–2014) dataset to (1) estimate overall and

91   seasonal patterns of capture probability, apparent survival, recruitment, and realized growth rate

92   of the brush mouse in a coastal-central California mixed-oak woodland, (2) determine the

93   relative contributions of survival and recruitment to population growth rate, and (3) explore the

94   role of rainfall and temperature in explaining variations in population vital rates. Our results

95   provide information on potential impacts of climate change on brush mouse population ecology,

96   and provide important management information for the species.

97   We expected that brush mouse survival, recruitment, and realized population growth rate

98   would exhibit seasonal fluctuations in response to the strongly seasonal patterns of rainfall on

99   our study site. Specifically, we hypothesized that brush mouse population parameters would be

4

100   positively influenced by rainfall, because water is a limiting resource in semi-arid environments

101   (Gutierrez et al. 2010, Previtali et al. 2009) and plant cover is an important habitat attribute for

102   the brush mouse. We expected that temperature would negatively influence brush mouse vital

103   rates due to higher energetic costs associated with foraging (Chen et al. 2015), although

104   temperature could positively affect recruitment by creating more favorable conditions for

105   reproduction (Andreo et al. 2009). We expected brush mouse vital rates to exhibit multi-annual

106   fluctuations corresponding to El Niño, which affects rainfall pattern in California. Finally, we

107   hypothesized that the population growth rate of the brush mouse would be influenced more by

108   recruitment than by survival because of the fast life history of the species (Heppell et al. 2000;

109   Oli and Dobson 2003; 2005; Oli 2004).

110   *Study Area* - We conducted the study at the Camp Roberts National Guard Post, a 17,000-

111   ha military facility located in coastal-central California (Figure 1). Our study area was located in

112   the backcountry of the Post, a roughly 4,000-ha matrix of undisturbed grassland, chaparral, and

113   woodland. Climate of the study area is Mediterranean, with cool, wet winters and warm, dry

114   summers. Annual rainfall is highly variable and is influenced by El Niño-La Niña oscillations.

115   More than 95% of the rainfall typically falls between October and April. During the study, mean

116   monthly rainfall during May to September was 0.33 cm (range: 0–4.75 cm, standard deviation:

117   5.36 cm) compared to a monthly mean of 5.26 cm during October to April (range: 0–31.27 cm,

118   standard deviation: 5.24 cm). The study area consisted of pure stands of blue oak (*Quercus*

119   *douglassii*), or on the more mesic sites, a mix of blue oak and coast live oak (*Q. agrifolia*). The

120   more mesic areas usually included a shrub layer of up to 35% cover (Tietje et al. 1997) and a

121   ground layer of introduced Mediterranean annual grasses (*Avena* spp.) and forbs.

122 *Field Methods* - In summer 1993, we laid out nine square 5.8-ha plots in areas with at

123 least 60% tree canopy cover. On each plot, we established with compass and tape a 17 x 17 grid

124 with 15-m intersections. We marked each of the 289 intersections per plot with a stake and a

125 survey flag with alphanumeric grid location. We trapped small mammals at each intersection in

126 May and in October. From October 1993 to October 1996, we trapped for 5 nights each session

127 for 7 trapping sessions (9 plots with 289 traps * 5 nights * 7 sessions = 91,035 trap nights). To

128 increase the number of sampling grids on the study area, in winter of 1997 we established twelve

129 1.1-ha plots with 8 x 8 trapping grid (Figure 1). Starting in May 1997, we trapped on these 12

130 plots and on 8 x 8 corners (1.1 ha) or two diagonal corners of six of the 5.8-ha plots. From May

131 1997 until May 2013, we sampled exclusively on these twenty-two 8 x 8 sampling grids for a

132 total of 22 plots with 8 x 8 traps * 3 nights * 33 sessions = 139,392 trap nights. In October 2013,

133 we trapped on 21 of the 22 plots for a total of 4,032 trap nights. Finally, in May 2014, we trapped

134 on 9 of the 22 plots for a total of 1,728 trap nights. We will refer to the period between the

135 October and May trapping sessions as a "season," which is either a summer season (5-month

136 period from May to September; the warm, dry season) or a winter season (the 7-month period

137 from October to April; the cool, wet season).

138 During each May and October sampling session, we placed one Sherman live trap (3 x

139 3.5 x 30-cm; H.B. Sherman Traps, Inc.) within 2 m of each grid intersection. To insulate trapped

140 animals from overnight cold and from the heating of the interior of the trap by early morning

141 sunshine, traps were placed in shade and covered with grass and other litter from the vicinity of

142 the trap. We baited traps with a mixture of rolled oats, corn, and barley laced with molasses. On

143 initial capture, we placed a laser-etched Monel 1005-1L1 animal tag and extra-long model XLK,

144 7.7 x 9.5 x 30.5 cm trap (National Band and Tag Co., Newport, Kentucky) in the animal's right

145   ear, and recorded trap location, tag number, species, sex, and age. Animals were released at site

146   of capture. All handling of animals followed the guidelines of the University of California,

147   Berkeley, Institutional Animal Care and Use Committee (UCB Permit # R-166). Trapping also

148   met the guidelines of the American Society of Mammalogists (Sikes et al., 2011).

149   *Capture-mark-recapture (CMR) Analysis* - We used Pradel's (1996) temporal symmetry

150   model to estimate apparent survival (ϕ), recapture (p) probabilities, and realized population

151   growth rate (λ). First, we fitted a series of base models where we allowed ϕ, p, and λ to be

152   affected by time (trapping session), year, season, and sex, and by the additive and interactive

153   effects of these variables; we estimated model parameters using the most parsimonious model in

154   the set (based on Akaike's information criterion corrected for small sample size AIC_c; Burnham

155   and Anderson 2002; Williams et al. 2002). After selecting the base model for each parameter, we

156   tested for the effect of individual climatic covariates on that parameter using the base model.

157   This second set of models allowed the model parameters to be affected by temperature, rainfall,

158   and sea-surface temperature anomaly (a measure of El Niño Southern Oscillation). We used a

159   similar modeling approach to test for the effects of climatic covariates on f using the ϕ–f

160   parameterization of Pradel's model (Williams et al. 2002). Since λ is based on the ratio of the

161   population sizes between two sampling periods, the measured population size must represent the

162   same sampled area. Otherwise, a bigger sampled area will yield a larger λ simply due to sampling

163   a bigger area. Since sampling in our study area varied slightly over the study period and only

164   remained constant from fall 1998 to spring 2013, we ran the ϕ-λ parametrization of Pradel's

165   model to obtain λ estimates for fall 1998 to spring 2012. In addition, because the first estimate of

166   λ is typically inestimable in time-specific models, we omitted the first estimate of λ. We

167   determined the relative contribution of ϕ and f to λ by calculating the proportional contribution

168   parameter γ (Nichols and Hines 2002, Schorr 2012). If γ is greater than 0.5, ϕ influences λ more

169   than f. We did not consider spatial grid-to-grid variation and conducted a single analysis that

170   combined data from all grids into one large population.

171   We performed all analyses with the program MARK (White and Burnham 1999) v. 6.2

172   through RMark (Laake 2013) in program R v. 2.2.0 (R Core Team 2014). We determined the

173   effect of climatic covariates by comparing AIC_c for models with and without a covariate, based

174   on 95% confidence intervals for the slope parameter defining the relationship between a

175   demographic parameter and the covariate(s).

176   *Climatic Covariates* - We extracted average daily temperature and precipitation for 1993–

177   2015 from the Paso Robles City NACC weather station (NOAA 2016), located in Paso Robles,

178   California, approximately 11 km southeast of the study area. We explored whether climatic

179   conditions during the current season or the previous season (one-lag) affected California mouse

180   vital rates (survival, recruitment, and growth). We used the following climatic variables: (i)

181   average temperature (temp_avg) (ii) coefficient of variation (CV) of temperature (temp_cv), and

182   CV of temperature with a one season lag (temp_cv_onelag), (iii) total seasonal rainfall

183   (rain_sum) and total seasonal rainfall with a one-season lag (rain_sum_onelag), and (iv) CV of

184   rainfall (rain_cv), and the CV of rainfall with a one-season lag (rain_cv_onelag). We reported the

185   estimates of slope parameters (β) based on the most parsimonious model that included a given

186   covariate (temperature, rain) for each vital rate (survival, recruitment, growth), regardless of

187   model structure for other demographic rates.

188   To examine effects of the El Niño Southern Oscillation (ENSO) on small mammal

189   population dynamics, we used the Oceanic Niño Index (ONI), the standard used by NOAA to

190   identify El Niño and La Niña events in the Pacific Ocean. An El Niño or La Niña is characterized

191   by five consecutive 3-month sea surface temperatures means above (for El Niño) or below (for

192   La Niña) a threshold of +0.5 °C (-0.5 °C), measured above the equatorial Pacific. We extracted

193   ONI values from the NOAA National Weather Service Climate Prediction Center

194   (http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml) and

195   information pertaining to the ENSO cycle from NOAA's Climate website

196   (https://www.climate.gov/enso).

197

198   *Results* - During the study (1993–2014), we captured 3,258 (1,634 female and 1,624 male)

199   brush mice 6,351 times. Per 1,000 trap nights, the highest number of mice trapped per session

200   was 80.73 in October 1998, and the lowest number of mice trapped was 1.15 in October 1996

201   (Figure 2).

202   *Demographic parameters without covariate effects*—Pradel's models indicated some

203   level of temporal variation in all demographic parameters: capture probability (p), apparent

204   monthly survival (ϕ), apparent monthly recruitment (f), and apparent monthly growth rate (λ).

205   Average capture probability was higher for females than for males, and higher in summer than in

206   winter for both sexes (Table 1). Average ϕ was 0.789 ± 0.005, and ϕ was higher in winter (0.848

207   ± 0.009) than in summer (0.764 ± 0.011; Table 1). Estimates for ϕ ranged from 0.620 ± 0.030

208   (summer 1994) to 0.946 ± 0.034 (winter 2005), and showed small fluctuations over the study

209   period, except when ϕ decreased from 0.924 (winter 2006) to 0.528 (summer 2007), a 57%

210   decrease (Figure 3). Monthly recruitment (f) varied substantially over time, ranging from $0.029 \pm$

211   0.047 to 0.538 ± 0.063 with an average of 0.175 ± 0.038, and was higher in summer ($0.240 \pm$

212   0.014) than in winter (0.137 ± 0.009; Table 1). The largest estimated f (0.538 ± 0.063) occurred in

213   winter 1996, and other high f rates occurred in summer 2005 (0.511 ± 0.097) and winter 2011

214   (0.414 ± 0.107). Estimated recruitment was lowest in the winters of 2009 (0.029 ± 0.047), 2005

215   (0.050 ± 0.037), and 2010 (0.068 ± 0.086), and time-specific f parameters were un-estimable

216   (confidence intervals from 0 to 1) during three seasons (Figure 3).

217   Our study population was stable during the 21 years of study (λ = 0.993 ± 0.032, ϕ-f

218   parametrization; Table 1), but estimated λ exhibited strong time-variation, particularly during

219   winter 1993 to summer 1997. The largest variation in estimated λ occurred when growth rate

220   increased from its lowest point during the 21-year period, 0.672 ± 0.052 in summer 1996, to 1.46

221   ± 0.08 in winter 1996 — a 118% increase (Figure 3). The most parsimonious model (based on

222   AIC_c) included an additive effect of sex and season for p, and a time effect on f, ϕ, and λ (Table

223   2a). Estimates for the proportional contribution parameter (γ) ranged from 0.515 to 0.969, with a

224   mean of 0.794 (SD = 0.097), and γ was consistently > 0.5.

225   *Individual climatic covariate effects on demographic parameters*—The most

226   parsimonious model for single covariate effects exhibited 92% of the AIC_c weight and included

227   the effect of variation in rainfall on ϕ and average temperature on f (Table 2b). Although the top

228   five models for ϕ included only variation in rainfall, rainfall with a one season lag, and average

229   temperature, all other variables except El Niño had significant effects on ϕ. Rainfall and variation

230   in rainfall with a one season lag had positive effects on ϕ, while average temperature, variation in

231   temperature, variation in rainfall, and rainfall with a one season lag had negative effects on ϕ

232   (Table 3; Figure 4c, 4d).

233   Although the top five most parsimonious models for f included average temperature,

234   rainfall, and variation in rainfall with a one season lag, all other variables except El Niño had a

235   significant effect on f. Average temperature, variation in temperature, variation in rainfall, and

236   rainfall with a one season lag had a positive effect on recruitment, while rainfall, rainfall with a

237   two season lag, and variation in rainfall with a one season lag had negative effects on f (Table 3;

238   Figure 4a, 4b). The effect of climatic covariates on λ was similar to the effect of climatic

239   covariates on ϕ. However, the overall strength of these effects was lower for λ than for ϕ.

240   Rainfall and variation in rainfall with a one season lag had a positive effect on λ, while average

241   temperature and variation in temperature had a negative effect on λ (Table 3).

242

243   *Discussion - Effect of rainfall on ϕ.*—Although the brush mouse population was stable

244   throughout the study period, there was substantial temporal variation in survival and recruitment,

245   and we posit that these fluctuations could be driven by climatic factors. Single-covariate models

246   showed a positive effect of rainfall on ϕ, and fluctuations in ϕ were highly correlated with

247   rainfall ($r = 0.44$, $p = 0.005$). The effects of precipitation on small mammal population vital rates

248   in semi-arid systems are generally well studied (Heske et al. 1994, Brown and Ernest 2002, Lima

249   et al. 2002, Meserve et al. 2003, Letnic and Dickman 2005), and a widely accepted hypothesis

250   posits that higher precipitation in semi-arid systems increases primary production, leading to an

251   increase in survival of small mammal populations (Heske et al. 1994, Lima et al. 2002, Shenbrot

252   and Krasnov 2001, Letnic and Dickman 2005, Yates et al 2002). Studies have associated

253   increased rodent densities with higher precipitation in various habitats (Brown and Ernest 2002,

254   Kuenzi et al. 2007, Meserve et al. 1995). Because the brush mouse is a shrub-habitat specialist,

255   its survival will be especially affected by precipitation and its effect on primary production,

256   which directly impacts food availability and refuge from predators (Bradley and Schmidly 1999,

257   Baker 1968, Kalcounis-Ruppell and Millar 2002). As an omnivore, the brush mouse consumes

258   fruits and seeds of a wide variety of plant species as well as insects, which are positively affected

259   by rainfall in resource-restricted semi-arid environments (Fuentes and Campusano 1985, Yang et

260 al. 2011). The brush mouse also depends on closed and dense cover for foraging and refuge from

261 weather and predators (Bradley and Schmidly 1999, Baker 1968, Kalcounis-Ruppell and Millar

262 2002). Emphasizing the crucial importance of vegetative cover for this species, a wildfire that

263 appreciably consumed brush cover led to a 90% decrease in brush mouse populations (Brehme et

264 al. (2011). Rainfall typically increases the amount of understory shrub and chaparral cover,

265 suggesting that the ability of the brush mouse to find food, survive in inclement weather, and

266 evade predators will increase with higher precipitation and lead to higher survival rates,

267 suggesting that abundance and access to food during high precipitation events could directly lead

268 to an increase in survival. Survival is thus an important population driver for the brush mouse

269 during periods of high rainfall.

270   *Effect of rainfall on f.*— In contrast to its effect on survival, covariate models showed a

271 negative influence of rainfall on recruitment. In our study, rainfall may have had a negative effect

272 on recruitment due to increased energetic costs incurred by reproductive females, or the

273 destruction of food stores and nesting sites used by reproductive females during times of heavy

274 precipitation. Although this is contrary to the general expectation that typically shows higher

275 recruitment in response to increasing precipitation (e.g., see Previtali et al. 2009, Shenbrot et al.

276 2010, Thibault et al. 2010b), the effect of precipitation is not necessarily linear or simple.

277 Extreme rainfall events can lead to catastrophic declines of small mammals, attributed to the

278 destruction of food stores and nesting sites (Valone and Brown 1995, Thibault and Brown 2008),

279 especially when located underground or just above the ground (shrubs or logs), habitats typically

280 utilized by brush mice for nesting. High rainfall, especially during cold periods, can also cause

281 abrupt declines in mouse populations (Calisher et al. 2005, Mills 2005, Llewellen and Vessey

282 1998, Garsd and Howard 1981, de Villafane and Bonaventura 1987, Mills et al. 1992). Such

283   unfavorable climatic conditions affect reproduction through mortality from direct exposure or

284   lack of access to food or shelter. Furthermore, exposure to heavy rainfall can result in

285   populations with smaller and fewer litters, possibly due to the higher energetic costs of

286   microclimate regulation for the female (Myers et al. 1985). It is important to note that in our

287   semi-arid study area, 96% of all precipitation occurred in the winter, and rainfall and temperature

288   showed high negative correlation ($r = -0.81$, $p < 0.001$). This indicates that precipitation

289   primarily occurred when it was colder, which could have had direct and indirect adverse effects

290   on recruitment as recruitment was positively correlated with temperature. Although the effect of

291   precipitation in winter could potentially be diluted by the lack of precipitation in summer,

292   conversely, a small amount of rain in summer can potentially have a big effect because of such

293   low amounts of precipitation in summer.

294   *Effect of temperature on ϕ and f.*—Temperature was negatively correlated with ϕ. We

295   suspect this is because foraging and juvenile dispersal would become energetically costly and

296   difficult to perform with higher temperatures, potentially leading to decreased ϕ (Bradley and

297   Schmidly 1999). Interestingly, average temperature had a significant positive effect on *f*. This

298   could be attributed to two plausible reasons: (1) *f* could likely increase with warmer temperatures

299   because brush mice can breed more frequently, especially during the winter (California

300   Department of Fish and Wildlife 2014, Bradley and Schmidly 1999); (2) higher temperatures in

301   spring and early summer increase primary productivity and allow female mice to expend less

302   energetic costs for foraging and ensuring a favorable microclimate for litters (through increased

303   vegetative cover for nests, which are typically found in trees and shrubs). Season and

304   temperature are known to have interactive and sometimes contradictory effects on small mammal

305   populations (Luis et al. 2010), however our results did not support an interactive effect of season

306   and temperature on brush mouse recruitment.

307   *Trade-offs between ϕ and f in the maintenance of population stability.*— Brush mouse

308   population growth rate (λ) was stable throughout the study ($\lambda = 0.993 \pm 0.032$). While ϕ was

309   positively affected by rainfall and negatively affected by temperature, *f* was positively affected

310   by temperature and negatively affected by rainfall (Figure 4). These contrasting effects of

311   climatic factors on vital rates suggests that the brush mouse employs alternating strategies in

312   maintaining population stability dependent on climatic conditions. Additionally, ϕ and *f*

313   estimates were highly negatively correlated ($r = -0.61$, $p = 0.002$), implying a trade-off between

314   ϕ and *f.* During hotter, drier seasons, the brush mouse invests in higher *f* as a means of

315   maintaining the population, whereas during cooler, wetter seasons, the brush mouse allocates

316   more energy towards ϕ to maintain population λ. Considered together, the brush mouse appears

317   to adopt a combination of coping mechanisms to ensure population stability.

318   The contribution of ϕ to λ was consistently higher than *f*, as inferred from the

319   proportional contribution parameter (Nichols and Hines 2002, Schorr 2012). The estimate of γ

320   averaged 0.82, i.e., on average, 82% of individuals in the current season are individuals that

321   survived from the previous season. Although small mammals are typically r-selected, where

322   population increase is fueled more by *f* than ϕ (Heppell et al. 2000b, Oli and Dobson 2003), the

323   brush mouse seems to be less r-selected than other small mammal species (Schorr 2012), due to

324   the relatively higher contribution of ϕ to λ for the species. This is interesting considering that

325   brush mouse life expectancy is typically less than one year (Abbott et al. 1999). The relatively

326   higher contribution of ϕ towards λ was also supported by the overall climatic effects on vital

327   rates. The effects of rainfall and temperature were similar for ϕ and λ (a positive effect of rainfall,

328   and a negative effect of temperature on both parameters). However, these effects were reversed

329   for f (a negative effect of rainfall, a positive effect of temperature). The relatively higher

330   contribution of ϕ towards λ than what is typically observed for small mammals is also supported

331   by the fact that the brush mouse prioritizes ϕ as a coping strategy in addition to f, and does not

332   rely primarily on f to ensure population stability.

333   *Climate change.*—Climate change forecast models suggest that climatic conditions will

334   become increasingly hotter and drier, with long dry periods punctuated by dramatic rainfall

335   events (Masson-Delmotte et al. 2018). These changes in climatic conditions will have differing

336   effects on brush mouse vital rates. Increasingly hotter and drier conditions may not bode well for

337   brush mice survival, especially because dry conditions typically worsen the effect of increased

338   temperatures. Our results suggest that brush mouse survival might decrease with climatic change.

339   Recruitment, on the other hand, might increase with hotter and drier conditions and become the

340   more dominant coping strategy in maintaining population stability. However, dramatic rainfall

341   events might have a negative effect on brush mouse recruitment, suggesting that an increase in

342   recruitment due to hotter and drier conditions might be tempered by more frequent, heavy

343   rainfall. Brush mice are also particularly dependent on ground and vegetative cover, mesic

344   environments and shrubs and trees for foraging and nesting (California Department of Fish and

345   Wildlife 2014). Since primary productivity is negatively affected by an increase in dry

346   conditions, climate change associated with more frequent and more intense droughts could be

347   detrimental to structural habitats that are important for the species. Climate models also predict

348   an increase in the frequency and magnitude of wildfires, especially in southern California and the

349   western Sierras (Westerling and Bryant 2008), which are extremely detrimental to brush mouse

350   populations. In addition to these, the invasive pathogen *Phytophthora ramorum*, which causes

351   Sudden Oak Death in tanoak and other oak species (McPherson et al. 2010), is one of the

352   pathogens that may become more widespread and harder to control with changing climatic

353   conditions (Brown and Allen-Diaz 2006). The spread of this pathogen could be especially

354   problematic for brush mice, which rely on tanoak acorns (Reid et al. 2013) and coast live oak

355   acorns (Kalcounis and Ruppell 2002), as a primary food source. However, the varying coping

356   strategies employed by the brush mouse in response to varying environmental conditions may

357   serve as a mechanism by which the species maintains resilience in the face of climate change.

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359   *Conclusions* - Our study was the first to apply Pradel's temporal symmetry models to

360   brush mouse populations and demonstrated the implementation of a modern demographic

361   modeling framework to quantify the effect of f and ϕ on population λ for a brush mouse

362   population. Although brush mouse population dynamics were influenced by localized climatic

363   effects, the overall population size remained stable and appeared resilient to annual and multi-

364   annual fluctuations. The brush mouse utilized a trade-off between survival and recruitment to

365   maintain population stability, using high f during warmer, drier seasons and high ϕ during cooler,

366   wetter seasons to sustain population size. Our results suggest that brush mouse survival might

367   decrease with climate change, while recruitment might increase with climate change and become

368   the more dominant coping strategy in maintaining population stability. However, since dramatic

369   rainfall events negatively affect brush mouse recruitment, an increase in recruitment due to hotter

370   and drier conditions might be tempered by more frequent, heavy rainfall. The varying coping

371   strategies employed by the brush mouse in response to varying environmental conditions may

372   serve as a mechanism by which the species maintains resilience in the face of climate change.

373   Brush mice play an important role in ecosystem processes, as they are extremely important prey

374   for a large variety of terrestrial and avian predators, including the federally threatened Mexican

375   spotted owl (Boyett 2001). Brush mouse are also reservoir hosts for the hantavirus, raising

376   important health concerns associated with rates of spread. Future investigations are needed to

377   build on our findings and examine other aspects such as predation, intra-guild competition and

378   the potential influence of spatial attributes on population dynamics, factors that, in addition to

379   our results, will likely have implications for the management and conservation of the species.

380   Furthermore, the trade-off between survival and recruitment could pose important consequences

381   for broader small mammal population dynamics and understanding mechanisms of species

382   resilience with climate change.

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574 **Table 1.** Overall, sex-specific and season-specific estimates of monthly apparent survival (ϕ),

575 capture probability (*p*), monthly recruitment (*f*), and realized monthly growth rate (λ) without

576 covariate effects estimated using Pradel's model fitted to brush mice capture-mark-recapture

577 data. Overall, sex-specific and season-specific estimates of ϕ were based on the third and fifth-

578 ranked model from Table 2a. Sex-specific and season-specific estimates of *f* were based on the

579 first, fourth, and twenty-fifth ranked model from Table 2a. Sex-specific and season-specific

580 estimates of λ were based on the first and third-ranked model from Supplementary Table S1.

	Survival (ϕ)	Recruitment (*f*)	Growth Rate (λ)	Capture probability (*p*)
Female	0.815 ± 0.005	0.177 ± 0.038	0.993 ± 0.033	0.700 ± 0.055
Male	0.815 ± 0.005	0.173 ± 0.038	0.993 ± 0.033	0.468 ± 0.046
Winter	0.848 ± 0.009	0.137 ± 0.009	1.009 ± 0.010	0.526 ± 0.048
Summer	0.764 ± 0.011	0.240 ± 0.014	0.973 ± 0.014	0.641 ± 0.053
Overall	0.817 ± 0.005	0.175 ± 0.038	0.993 ± 0.032	0.584 ± 0.051

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594   **Table 2a-b.** Model selection results for the Pradel's model fitted to capture-mark-recapture data

595   for brush mice (*Peromyscus boylii*), testing for the effect of time (trapping session), year, season

596   (winter or summer), and sex (male or female). Parameters are: ϕ = apparent survival probability;

597   *p* = capture probability; and λ = realized population growth rate. The number of parameters (*K*),

598   difference in Akaike's information criterion corrected for small sample size between a given

599   model and the top-ranked model (ΔAICc), and the relative model weight are also given. The five

600   best-supported models are presented. A plus sign (+) indicates additive and an asterisk (*)

601   indicates both additive and interactive effects of the covariates involved. (A) Models for monthly

602   apparent survival (ϕ) and recruitment (*f*) rates without covariate effects. (B) Models testing for

603   the singular effect of climatic covariates on ϕ and *f*.

604   **Table 2a.**

Model	*K*	Δ**AICc**	**Weight**
φ(~time) *p*(~season + sex) *f*(~time)	85	0	0.441
φ(~time) *p*(~season * sex) *f*(~time)	86	1.808	0.179
φ(~time + sex) *p*(~season + sex) *f*(~time)	86	2.182	0.148
φ(~time + sex) *p*(~time) *f*(~time)	86	3.772	0.067
φ(~season) *p*(~season * sex) *f*(~time)	87	3.8528	0.064

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606   **Table 2b.**

Model	*K*	Δ**AICc**	**Weight**
φ(~rain_cv) *p*(~season + sex) *f*(~temp_avg)	46	0	0.921
φ(~rain_cv) *p*(~season + sex) *f*(~rain_sum)	46	5.977	0.046389
φ(~rain_sum_onelag) *p*(~season + sex) *f*(~rain_cv_onelag)	46	7.172	0.025523
φ(~rain_sum_onelag) *p*(~season + sex) *f*(~temp_avg)	46	12.822	0.001514
φ(~temp_avg) *p*(~season + sex) *f*(~temp_avg)	46	13.057	0.001346

607 **Table 3.** The effect of climatic covariates on apparent survival (φ), recruitment (*f*), and realized

608 population growth rate (λ) of brush mice (*Peromyscus boylii*) in a coastal-central California

609 mixed-oak woodland. We report the estimate of slope parameters (β ± SE) based on the most

610 parsimonious model that included a given covariate for each demographic rate, regardless of

611 model structure for other demographic rates. Estimates in bold indicate that 95% CI for β do not

612 include zero.

Demographic parameter	Climate covariate	β ± SE
Survival (φ)	Temp_avg	**-0.12 ± 0.05**
	Temp_cv	**-0.07 ± 0.03**
	Rain_sum	**0.15 ± 0.04**
	Rain_sum_onelag	**-0.13 ± 0.03**
	Rain_cv	**-0.14 ± 0.03**
	Rain_cv_onelag	**0.08 ± 0.04**
	El Niño	-0.03 ± 0.02
Demographic parameter	**Climate covariate**	**β ± SE**
Recruitment (*f*)	Temp_avg	**0.27 ± 0.05**
	Temp_cv	**0.076 ± 0.037**
	Rain_sum	**-0.17 ± 0.045**
	Rain_sum_onelag	**0.193 ± 0.031**
	Rain_cv	**0.147 ± 0.034**
	Rain_cv_onelag	**-0.091 ± 0.034**
	El Niño	-0.004 ± 0.02
Demographic parameter	**Climate covariate**	**β ± SE**
Growth rate (λ)	Temp_avg	0.008 ± 0.009
	Temp_cv	-0.003 ± 0.003
	Rain_sum	**0.033 ± 0.005**
	Rain_sum_onelag	**0.070 ± 0.006**
	Rain_cv	**-0.014 ± 0.004**
	Rain_cv_onelag	**-0.019 ± 0.004**
	El Niño	0.009 ± 0.01

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Figure 1. Map of the study area. Trapping was carried out on nine 5.8-ha 17x17 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. 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

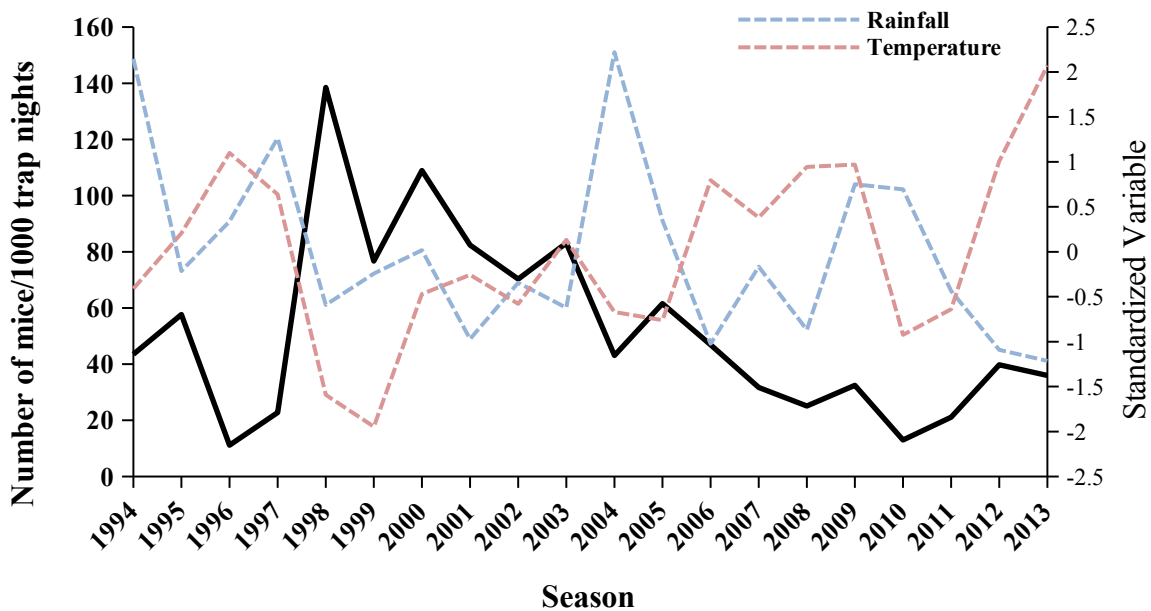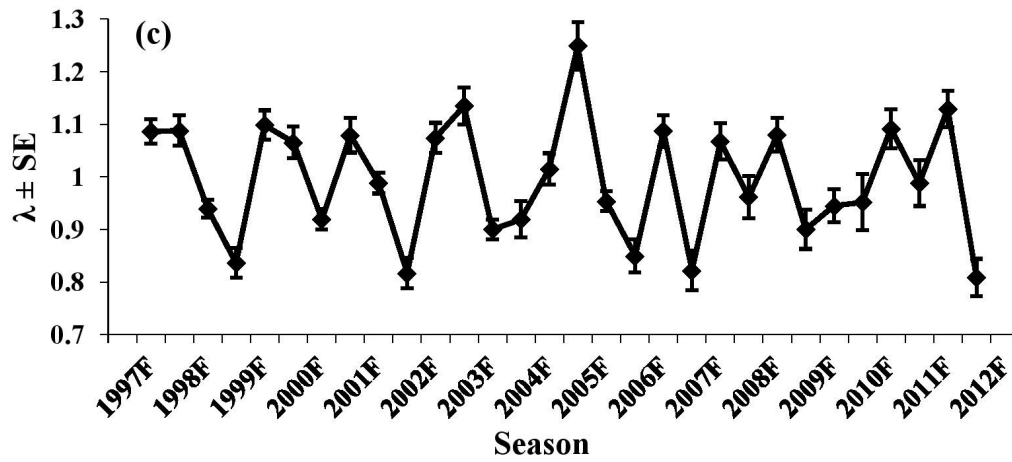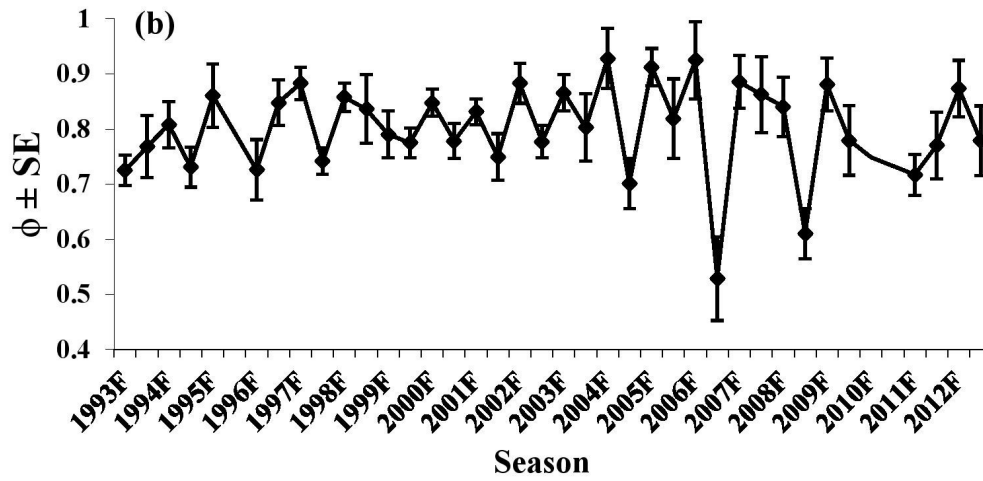distribution of the brush mouse (Peromyscus boylii; grey shading) in California, USA
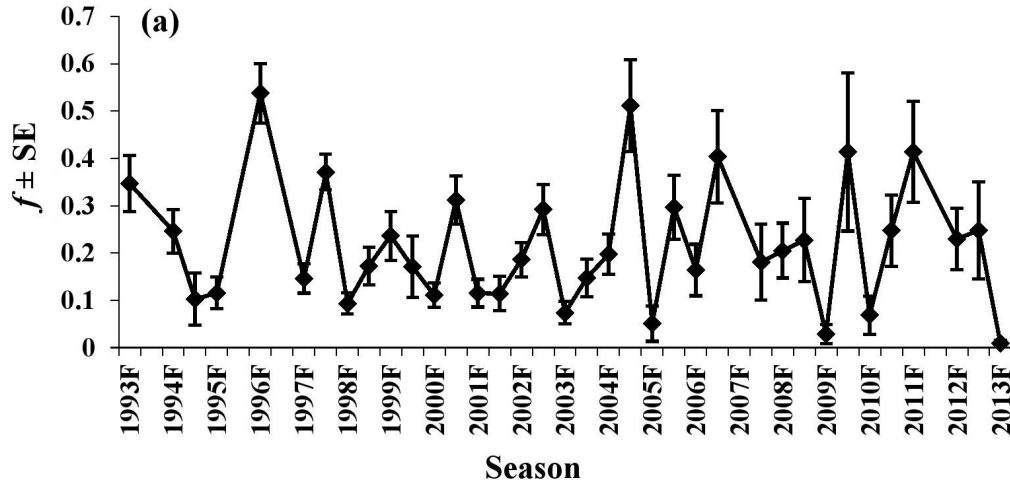
640   **Figure 2.** The minimum number of brush mice/1000 trap nights captured during spring and fall

641   sessions on nine 5.8-ha study plots (17 x 17 sampling grid) during October 1993 to October

642   1996, on 22 1.1-ha study plots (8 x 8 sampling grid) during May 1997 to May 2014 for a total of

643   232,155 total trap nights at Camp Roberts, CA. The blue and orange dotted lines represent a

644   standardized rainfall and temperature index.

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656 **Figure 3a-c.** Estimates of (a) monthly apparent survival (ϕ) (b) recruitment rate (*f*), and (c)

657 realized population growth rate (λ) of brush mice (*Peromyscus boylii*) at Camp Roberts,

658 California, from winter 1993 to winter 2013 for ϕ and *f*, and from summer 1997 to winter 2012

659 for λ, based on the most parsimonious model (Table 2a, 2b). Sampled area varied over the course

660 of the study, but was constant from winter 1997 to summer 2012. Thus, estimates for λ were

661 produced for a shorter time interval because λ must be based on constant-size areas. The first

662 estimate for λ is excluded because it is typically inestimable in time-specific models. Spring

663 season estimates follow winter seasons and are not labeled on the axis.

666 **Figure 4.** Effects of climatic variables (z-transformed) on survival and recruitment of brush mice

667 (*Peromyscus boylii*) at Camp Roberts, California based on the most parsimonious model that

668 included the given covariate for each demographic rate; (a) relationship between rainfall and

669 recruitment (*f*); (b) relationship between temperature and recruitment (*f*); (c) relationship

670 between rainfall and survival (ϕ); (d) relationship between temperature and survival (ϕ).

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