POPULATION VIABILITY OF *Pediocactus bradyi* (Cactaceae) IN A CHANGING CLIMATE

DANIEL F. SHRYOCK\(^2,4\), TODD C. ESQUE\(^2\), AND LEE HUGHES\(^3\)

\(^2\)U.S. Geological Survey, Western Ecological Research Center, 160 N. Stephanie Street, Henderson, Nevada 89014 USA; and
\(^3\)U.S. Bureau of Land Management, AZ Strip Field Office, St. George, Utah 84790 USA

- **Premise of the study:** A key question concerns the vulnerability of desert species adapted to harsh, variable climates to future climate change. Evaluating this requires coupling long-term demographic models with information on past and projected future climates. We investigated climatic drivers of population growth using a 22-yr demographic model for *Pediocactus bradyi*, an endangered cactus in northern Arizona.
- **Methods:** We used a matrix model to calculate stochastic population growth rates \(\lambda_s\) and the relative influences of life-cycle transitions on population growth. Regression models linked population growth with climatic variability, while stochastic simulations were used to (1) understand how predicted increases in drought frequency and extreme precipitation would affect \(\lambda_s\), and (2) quantify variability in \(\lambda_s\) based on temporal replication of data.
- **Key results:** Overall \(\lambda_s\) was below unity (0.961). Population growth was equally influenced by fecundity and survival and significantly correlated with increased annual precipitation and higher winter temperatures. Stochastic simulations increasing the probability of drought and extreme precipitation reduced \(\lambda_s\), but less than simulations increasing the probability of drought alone. Simulations varying the temporal replication of data suggested 14 yr were required for accurate \(\lambda_s\) estimates.
- **Conclusions:** *Pediocactus bradyi* may be vulnerable to increases in the frequency and intensity of extreme climatic events, particularly drought. Biotic interactions resulting in low survival during drought years outweighed increased seedling establishment following heavy precipitation. Climatic extremes beyond historical ranges of variability may threaten rare desert species with low population growth rates and therefore high susceptibility to stochastic events.

**Key words:** Cactaceae; climate change; demographic model; desert species; drought; elasticity; life table response experiments; matrix model; rare species; stochastic population growth rate.

Species inhabiting deserts are adapted to variable climatic conditions, exhibiting episodic demographic patterns strongly linked with pulses of resource availability (Chesson et al., 2004). Rare, stochastic events shape long-term population dynamics for many desert species (Miriti et al., 2007), including El Niño-driven precipitation pulses triggering recruitment (Holmgren et al., 2006) and severe droughts causing mortality (Miriti et al., 2007). Changing climates over the next century are expected to increase temperatures and shift the frequency and intensity of extreme climatic events (Allan and Soden, 2008; IPCC, 2013), with potentially large impacts to vulnerable species and biodiversity. Given that desert species are already adapted to variable resource pulses and harsh conditions, a key question concerns the extent to which these species will be demographically resilient to future changes in climate (Salguero-Gómez et al., 2012). Common approaches for predicting species' susceptibility, such as bioclimatic habitat models (e.g., Téllez-Valdés and Dávila-Aranda, 2003), generally lack an underlying demographic basis to account for differences in species' physiological tolerances, regeneration rates, and dispersal capabilities—all of which could influence response (Fordham et al., 2012). Long-term demographic information is sorely needed to understand how desert species have responded to past climatic fluctuations and enable predictions for how future climatic changes will affect demographic processes. In particular, few studies have developed long-term demographic models to understand the potential effects of climate change on populations of rare desert species (Salguero-Gómez et al., 2012).

In the arid southwestern United States, global and regional climate models have predicted increased temperatures (Christensen and Lettenmaier, 2007), decreased annual precipitation (Gao et al., 2012), increased drought (Seager et al., 2007; Dai, 2013), and more extreme precipitation events (Dominguez et al., 2012). Climatic changes may already be affecting this region (Cook et al., 2004), as severe droughts and above-average temperatures from 2002 to 2003 precipitated regional-scale vegetation die-offs (Breshears et al., 2005; Miriti et al., 2007).

Altered climatic conditions will likely have the largest impacts on species with low population growth, narrow habitat requirements, and limited dispersal ability (Davis and Shaw, 2001)—all characteristics of the Cactaceae (Godínez-Alvarez et al., 2003), a family represented by numerous species in the southwestern United States, both rare and common. The ability for cacti to persist under changing climates will likely depend on the intrinsic sensitivity of different life-cycle stages to altered environmental conditions (Moritz and Agudo, 2013). As with...
other desert species, cacti persist in harsh, variable environments by coupling low fecundity with high survival and long lifespans (Godínez-Alvarez et al., 2003). Favorable climatic conditions may result in peaks of recruitment, but many factors—including drought, biotic interactions, and freezing temperatures—can significantly reduce the survival of seedling cohorts (Jordan and Nobel, 1981; Dreznner and Lazarus, 2008). Whether cacti will be resilient to changes in climate may be a good indicator for the susceptibility of other desert species, and is also an issue of conservation concern, as many cactus species are rare or threatened (Anderson et al., 1994).

Stage-structured population matrix models provide a means for assessing population growth rates and the relative influence of different life-history stages and may also be used to generate stochastic projections of population growth under various scenarios of environmental and demographic variability (Caswell, 2001). Coupling stochastic matrix models with historical climate information and robust future climatic projections may be a useful approach for determining the susceptibility of populations and specific life-history stages to climate change (Salguero-Gómez et al., 2012), particularly if demographic models can be made spatially explicit (Keith et al., 2008). However, this approach requires long-term demographic data sets to be effective, whereas most demographic studies have been of short duration due to various constraints (Crone et al., 2011).

An important question in this regard, particularly for desert species with episodic demographic patterns, is the length of time required to derive accurate estimates of stochastic population growth and other measures used to determine the influence of life-history stages, such as elasticity values (Fieberg and Ellner, 2001). This question has received limited empirical treatment in the literature (but see Doak et al., 2005) despite its obvious relevance for predictions of species’ responses to climate change based on demographic models.

Matrix models have been developed for a number of threatened cacti in recent years, particularly for species in Mexico (e.g., Esparza-Olguín et al., 2002; Valverde et al., 2004; Valverde and Zavala-Hurtado, 2006; Jiménez-Sierra et al., 2007; Martínez et al., 2010). However, most studies are of insufficient length to quantify climatic influences on demographic processes, instead focusing on habitat destruction, which may be a more immediate threat (e.g., Ureta and Martorell, 2009). At present, little demographic information is available for many threatened or endangered cacti endemic to the southwestern United States, where large-scale climate changes are expected over the next century. As an example, there have been no peer-reviewed studies concerning the population biology of any member of the genus _Pediocactus_, which includes seven species with threatened or endangered status through the U. S. Fish and Wildlife Service (USFWS) or the state of Arizona (USDA Plants Database, http://plants.usda.gov).

_Pediocactus bradyi_ Benson is a semiglobose cactus classified as an endangered species by the U. S. Fish and Wildlife Service since 1979. Discovered in 1958, _P. bradyi_ is thought to occur exclusively on soils characterized by white limestone chips of the Kaibab Formation, underlain by Moenkopi shale and sandstone (L. Hughes, personal observation; USFWS, 1979, 1985), and is known only from scattered populations along the rim of Marble Canyon in northern Arizona. Along with other members of the genus, _P. bradyi_ is unique for its ability to retract beneath the ground surface, likely in response to drought conditions or unfavorable temperatures (L. Hughes, personal observation). Contractile roots have been noted in several cactus genera, but only confirmed experimentally as a high temperature avoidance strategy in one species (_Ariocarpus fissuratus_; Garrett et al., 2010). It is unclear whether retraction of _P. bradyi_ is due to root contraction or tissue desiccation. However, retraction below ground may give _P. bradyi_ one mechanism for coping with a changing climate.

In this study, we develop a population matrix model for _P. bradyi_ based on demographic monitoring conducted at four populations over 22 yr. Our primary research objectives were to determine (1) the stochastic population growth rate of _P. bradyi_, (2) the influence of different life-cycle stages on overall population growth, and (3) how climate influences population growth. However, the temporal scope of our data set also allowed us to address two key areas of uncertainty for arid environments facing global change: (1) the degree to which changes in the frequency or intensity of extreme climatic events might affect population processes for rare desert species, and (2) the temporal replication necessary to derive accurate estimates of stochastic population growth ($\lambda$) for desert species with episodic demographic patterns. To address the first, we conduct stochastic simulations varying the probability of extreme climatic events that occurred during monitoring, including drought and El Niño related precipitation pulses. For the second, we use stochastic simulations to calculate the degree of variability surrounding $\lambda$ estimates based on the length of the monitoring period.

**MATERIALS AND METHODS**

**Study species**—_Pediocactus bradyi_ is a semiglobose cactus, generally with single stems (though rarely, 2–4 stems) reaching a maximum diameter of approximately 60 mm (Benson, 1969). Stems rarely extend more than 30 mm above the ground and may retract below ground in summer and winter months. Flowering occurs from late March to early April. An individual cactus typically produces 1–3 flowers depending on stem size, with stems beginning to flower when they reach approximately 15 mm in diameter (Appendix S1, see Supplemental Data with the online version of this article). The yellow flowers (up to 2 cm long) are born on the tip of the tubercle at the apex of stems. Fruits are green brown and dehiscent by a vertical slit. _Pediocactus bradyi_ is known only from scattered populations on U. S. National Park Service, Navajo Nation, and U. S. Bureau of Land Management lands along the rim of Marble Canyon, near Lees Ferry, Arizona.

**Monitoring sites**—Four plots with populations were established between 1985 and 1988 on lands administered by the U. S. Bureau of Land Management (BLM). The four plots, referred to as Badger Creek, Soap Creek, North Canyon East, and North Canyon West, are rectangular but differ in size: Badger Creek (28 × 30 m), Soap Creek (10 × 90 m), North Canyon East (30 × 35 m), and North Canyon West (1177 m a.s.l.) and Soap Creek (1247 m a.s.l.) plots are farthest north but lowest in elevation and separated by approximately 5.6 km. The North Canyon East and West plots (1478 m) are separated by only 0.25 km and located approximately 15.7 km southeast of the Soap Creek plot and 21.1 km southeast of Badger Creek. Although the total number of cacti varied substantially across the 22 yr of our study, cactus densities (individuals/m²) averaged 0.15 for the Badger Creek plot, 0.11 for Soap Creek, 0.06 for North Canyon East, and 0.05 for North Canyon West. Within plots, the cacti generally occurred in small, widely spaced clumps. Surrounding vegetation is sparse and dominated by low shrubs and grasses, including _Atriplex confertifolia_, _Gutierrezia sarothrae_, and _Achnatherum hymenoides_. Annual grasses, including invasive species of _Bromus and Schismus_, are also common. Average annual precipitation (±SD) at the closest long-term weather station to our plots (Lees Ferry, AZ, approximately 5 km north of Badger and Soap creek, and 25 km northeast of North Canyon East and West; http://www.wrc.cdi.int) is 153.2 ± 49.5 mm, with an average of 46 mm occurring as snowfall. The average annual maximum temperature is 24.7°C, while the average annual minimum temperature is 9.3°C.
Monitoring was conducted annually from 1988 to 2010 in all plots. Sampling occurred from late March to early April in all years except 1992, when sampling took place in October. Within each plot, all cacti were given numbered tags and tracked from year to year. Diameters of tagged cacti at their widest point were measured annually, along with the number of flowers or fruits produced. Height was not measured because *P. bradyi* frequently changes height in relation to the soil surface. Plots were closely searched for recruits each year and newly found cacti were tagged and measured. Causes of mortality (e.g., herbivory) were recorded when they could be determined. Because *P. bradyi* is able to retract below ground, tags were left in place at least 5 yr after cacti were last seen to ensure that they were not simply retracted.

**Demographic model**—For an estimate of the average longevity of *P. bradyi*, we calculated a survival curve with point-wise confidence intervals using the Kaplan-Meier estimator. We then constructed a demographic model using Lefkovitch size-classified transition matrices (Lefkovitch, 1965), which are appropriate for species of Cactaceae because fecundity and survival probabilities both increase with size (Godínez-Alvarez et al., 2003). Transition matrices allow projections of future population size based on an initial vector of population counts for each size-class (Caswell, 2001). This procedure follows the equation: $n_t = A^n n_0$, where $A$ is a square matrix and $n$ is the number of individuals in each size class at times $t$ and $t + 1$. The elements $(a_{ij})$ of matrix $A$ represent fecundities and transition probabilities between size classes at the $t$th row and $t$th column. The dominant eigenvalue of $A$ is the finite rate of population increase $\lambda$, while the left and right eigenvectors are used in calculations of stationary values, which may be interpreted as the relative contributions of each matrix element $a_{ij}$ to $\lambda$ (Caswell, 2001). Elasticity values sum to one and may be added to compare the relative importance of different processes, including stasis (remaining in the same size class), growth, and fecundity (de Kroon et al., 2000).

Size classes used in transition matrices should be narrow enough to capture the range of variability in transition rates, but broad enough so that classes retain enough individuals for accurate estimation of population parameters (Caswell, 2001). On the basis of these criteria, we classified *P. bradyi* into three size classes: small (1–15 mm stem diameter), medium (16–30 mm) or large (31–60 mm). The cutoff point for the first size class (15 mm) corresponds to the size at which cacti begin to produce flowers (Appendix S1). In cases where cacti were retracted below ground and could not be measured during a census, individuals were retained in the same size class until the next recorded measurement. Cacti that were noted as retracted and never again found were considered mortalities.

We were unable to include a matrix category representing a seed class because germination rates, seed bank persistence, and average numbers of seeds per fruit are unknown for *P. bradyi*. Fecundity matrix entries were therefore calculated as the relative contribution of individuals in a size class to the following year’s reproductive output (sensu Fréville et al., 2004). Because flowering events were not consistently captured every year, we combined overall probabilities of flowering for each size class with a logistic regression equation linking stem diameter with flower production. Fecundities were thus calculated by:

$$\frac{F_f F_e}{N_f} = R,$$

where $F_f$ represents the probability of flowering for a size class, $F_e$ represents the predicted number of flowers derived from logistic regression, $N_f$ represents the total number of flowers predicted to occur within a plot, and $R$ represents the number of recruits found in the next census for that plot. The logistic equation was: $p = \exp(-3.41 + 0.1\text{-Width}) / (1 + \exp(-3.41 + 0.1\text{-Width}))$ and accurately predicted 70% of cases ($P < 0.0001$).

Annual transition matrices were calculated for each plot and year combination ($4 \times 22$ yr). Overall pooled transition matrices for each plot were then calculated by pooling data across all 22 annual censuses. For an overall population estimate, we pooled data across plots and calculated pooled annual transition matrices ($n = 22$) along with an overall pooled transition matrix including all plots and years. In these calculations, we chose to pool data rather than average transition matrices across years to avoid giving undue weight to transitions with fewer cacti and thus higher demographic variability. Deterministic population growth rates ($\lambda$) were calculated through eigen analysis of transition matrices for each plot × year combination and for pooled transition matrices from individual plots and the overall pooled data set (Caswell, 2001). Elasticity values were also calculated through eigen analysis, but only for pooled transition matrices from plots and the overall data set.

**Life table response experiments (LTER)**—Elasticity values for transition matrices are known to vary within populations from year to year, particularly for species with variable recruitment (Menges, 2000), and are correlated with $\lambda$ (Silvertown et al., 1996). Life table response experiments (LTERs) are simulations representing the impacts of perturbations on population growth rates (Caswell, 2001). We used the overall pooled transition matrix as reference and performed LTERs to identify transition rate contributions to $\lambda$ in years of contrasting population growth rates by separating annual transition matrices from the pooled data set into three groups based on $\lambda$ high growth rate ($\lambda > 1.01$), low growth rate ($\lambda < 0.99$), and stable (0.99 < $\lambda < 1.01$). We then pooled the annual data within each group and calculated pooled transition matrices ($n = 3$), which served as the treatment matrices in the LTER.

**Population growth in relation to climate**—Climate records were obtained from the nearest long-term weather station to our plots, located at Lees Ferry, AZ (3652 N, 11135 W; elevation 980 m a.s.l.). Climate variables derived for analysis included: annual precipitation (total from April to March, corresponding to the census period), winter minimum temperature (December–January average), summer maximum temperature (June–August average), and spring maximum temperature (March–May average), along with 2 yr averages calculated for each of these variables (census year averaged with preceding census period). We chose these variables because annual precipitation and temperature are known to influence growth and establishment in a number of cacti (Jordan and Nobel, 1982; Drezner and Balling, 2002; Drezner and Lazarus, 2008).

We applied hierarchical partitioning (HP; Chevan and Sutherland, 1991) to identify climate variables exerting the greatest influence on annual population growth rates ($\lambda$) and mortality. HP is a regression technique that estimates the independent and joint influence of each predictor variable using the full hierarchy of possible models and expresses these influences as a goodness-of-fit measure (e.g., $R^2$, Mac Nally, 2000). Unlike ordinary multiple regression, HP is not sensitive to correlation between explanatory variables. The statistical significance of variables’ independent contributions can be determined via randomization and $z$ scores (Mac Nally, 2002). Due to the low sample size ($n = 22$), we chose to investigate interactions between variables. We also calculated HP models for the set of four single-year climate terms and for the set of 2-yr average terms separately. Annual mortality counts were log-transformed before performing HP. Variables found to be significant in HP models were further investigated using linear regression.

**Stochastic simulations**—We calculated stochastic population growth rates ($\lambda$) for the pooled data set and for each plot separately using whole-matrix selection. We chose this method because it preserves the within-year correlation structure of demographic processes, is easily reproducible (Kaye and Pyke, 2003), and can be useful for modeling the effect of discrete events, as we do in this study (Fieberg and Ellner, 2001). Also, we did not find evidence of temporal autocorrelation in $\lambda$ values, which could reduce the accuracy of whole-matrix selection. For each set of 22 annual transition matrices (pooled data + four plots), $\lambda$ was calculated by averaging the log ($\lambda$) values over 50 000 random matrix selections. Confidence intervals for these estimates were calculated by taking the 2.5th and 97.5th percentiles of the simulated distribution of log ($\lambda$) values.

We also performed whole-matrix selection simulations to see how changes in the frequency of extreme climatic events—as predicted for the southwestern United States (Domínguez et al., 2012; IPCC, 2013)—might affect stochastic population growth rates for *P. bradyi*. These simulations were performed using only data pooled across plots, which provided the most complete estimates for annual transition probabilities and also made analytical sense because we did not have separate climatic data for each plot. Two broad climate change scenarios were considered: (1) increased probability of drought and (2) increased probability of both drought and extreme precipitation events. To represent drought, we chose the 1989–1990 and 2008–2009 census periods, corresponding to the lowest precipitation levels recorded during our study. Similarly, extreme precipitation was represented by the 1992–1993 and 2004–2005 census periods, corresponding to the highest recorded precipitation. For each scenario, $\lambda$, was calculated as described above, but with increased selection probabilities for the transition matrices representing extreme events. Specifically, simulations representing (1) above increased the probability of selection for the 1989–1990 and 2008–2009 transition matrices, while simulations representing (2) increased selection probability for both the 1989–1990 / 2008–2009 transition matrices and the 1992–1993 / 2004–2005 transition matrices. In each case, matrix selection probabilities were gradually increased through eight different probability levels: 1.25$x$ (e.g., 1.25/22 or 0.057), 1.5$x$, 1.75$x$, 2$x$, 2.25$x$, 2.5$x$, 2.75$x$, and 3$x$. However, these increased selection probabilities were split
evenly across the two transition matrices representing drought or extreme precipitation in each simulation. For example, the probability of selection for each transition matrix representing drought at the 1.25x probability level was 0.125/2, or 0.051.

Similarly, we calculated quasi-extinction risks, defined as the probability of a future population size of <10 cacti after 75 yr, using whole-matrix selection simulations for both an equal probabilities scenario (i.e., equal selection probability for each annual transition matrix, representing observed conditions) and for the 1.5x, 2x, 2.5x, and 3x probability levels of increased drought. As with the calculation of λ, we used only data pooled across plots. In each simulation, future population size after 75 yr was estimated through 5000 runs of randomized 75 yr projection intervals, in which transition matrices were randomly selected (based on the selection probabilities described) 75 times for each interval. The proportion of the 5000 runs that resulted in a future population size of <10 cacti was then calculated. This procedure was repeated 10 times, and the quasi-extinction risk was taken as the average of these 10 proportions. All of the 75-yr projection intervals began with an initial vector of population counts in each size class that was then multiplied by 75 randomly selected transition matrices. To estimate a minimum viable population size for each scenario, we performed simulations using a range of initial population counts, from n = 100 to 2000, distributed among size classes according to the stable stage distribution of the overall pooled transition matrix (small = 0.3, medium = 0.5, large = 0.2; Caswell, 2001).

Variability in estimates of λ—Population growth rates exhibit a high degree of spatiotemporal variability, particularly for desert species with episodic demographic patterns. We therefore devised a method to quantify the amount of uncertainty in estimates of λ, based on the length of the monitoring period. Random sets of consecutive annual transition matrices, ranging in length of time from 2 to 18 yr (e.g., 2 consecutive yr, 4 consecutive yr, etc.) were selected with replacement from the pool of 152 pooled annual transition matrices. For each randomly selected set of matrices, the stochastic population growth rate (λ) was calculated following the procedure described above (see Stochastic simulations). This process was repeated 1000 times for each length of time (2, 4, 6 yr, etc.), creating a sampling distribution of λ estimates. We then calculated the standard deviations of these λ distributions for each time length. These standard deviations allow an assessment of the variability in estimates of the stochastic growth rate of *P. bradyi* based on the number of years of monitoring data available.

Statistical procedures—All calculations were performed in R version 3.0.3 (R Development Core Team, 2014). The survival curve for *P. bradyi* was calculated using the R package “survival” ( Therneau and Lumley, available at http://CRAN.R-project.org/package=survival). Matrix projections, LTREs, and simulations were calculated using the R package “survival” ( Therneau and Lumley, available at http://CRAN.R-project.org/package=survival). Simulations were performed using the R package “survival” ( Therneau and Lumley, available at http://CRAN.R-project.org/package=survival). The HP was performed using the R package hier.part (Walsh and Mac Nally, available at http://CRAN.R-project.org/package=hier.part.

RESULTS

A total of 1049 cacti were tagged and measured throughout the study, with annual population size ranging from a low of 152 cacti in 1991 to a high of 311 in 2002 ( Table 1 ). Survivorship for *P. bradyi* was lowest during the first 5 yr of life and after approximately 15 yr, with higher survivorship exhibited by cacti in between this age range (Appendix S2, see online Supplemental Data). The median survival time was 8 yr, with a 95% confidence interval of 6–11 yr. However, 31 cacti survived for over 15 yr, with higher survivorship exhibited by cacti in between this age range (Appendix S2, see online Supplemental Data). The median survival time was 8 yr, with a 95% confidence interval of 6–11 yr. However, 31 cacti survived for over 15 yr, with higher survivorship exhibited by cacti in between this age range (Appendix S2, see online Supplemental Data). The median survival time was 8 yr, with a 95% confidence interval of 6–11 yr. However, 31 cacti survived for over 15 yr, with higher survivorship exhibited by cacti in between this age range (Appendix S2, see online Supplemental Data).

Demographic model—The largest transition probabilities in the overall pooled transition matrix were associated with stasis (Table 2), with probabilities above 60% for every size class.

<table>
<thead>
<tr>
<th>Census</th>
<th>N</th>
<th>Pooled</th>
<th>Badger</th>
<th>Soap</th>
<th>East</th>
<th>West</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988–1989</td>
<td>222</td>
<td>0.960</td>
<td>0.923</td>
<td>1.026</td>
<td>0.938</td>
<td>1.000</td>
</tr>
<tr>
<td>1989–1990</td>
<td>218</td>
<td>0.722</td>
<td>1.000</td>
<td>1.086</td>
<td>0.154</td>
<td>0.500</td>
</tr>
<tr>
<td>1990–1991</td>
<td>189</td>
<td>0.760</td>
<td>0.965</td>
<td>1.000</td>
<td>0.273</td>
<td>0.680</td>
</tr>
<tr>
<td>1991–1992</td>
<td>152</td>
<td>0.932</td>
<td>0.589</td>
<td>0.984</td>
<td>0.766</td>
<td>1.000</td>
</tr>
<tr>
<td>1992–1993</td>
<td>168</td>
<td>1.270</td>
<td>1.358</td>
<td>1.050</td>
<td>1.000</td>
<td>1.509</td>
</tr>
<tr>
<td>1993–1994</td>
<td>199</td>
<td>1.008</td>
<td>0.912</td>
<td>0.988</td>
<td>0.935</td>
<td>1.145</td>
</tr>
<tr>
<td>1994–1995</td>
<td>208</td>
<td>1.005</td>
<td>1.091</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>1995–1996</td>
<td>206</td>
<td>1.035</td>
<td>0.920</td>
<td>1.059</td>
<td>0.985</td>
<td>0.896</td>
</tr>
<tr>
<td>1996–1997</td>
<td>248</td>
<td>1.075</td>
<td>1.024</td>
<td>0.879</td>
<td>1.000</td>
<td>0.969</td>
</tr>
<tr>
<td>1997–1998</td>
<td>273</td>
<td>1.033</td>
<td>0.863</td>
<td>0.996</td>
<td>1.150</td>
<td>1.166</td>
</tr>
<tr>
<td>1998–1999</td>
<td>296</td>
<td>0.991</td>
<td>1.079</td>
<td>1.022</td>
<td>1.000</td>
<td>0.954</td>
</tr>
<tr>
<td>1999–2000</td>
<td>291</td>
<td>0.990</td>
<td>0.952</td>
<td>0.966</td>
<td>1.029</td>
<td>1.114</td>
</tr>
<tr>
<td>2000–2001</td>
<td>277</td>
<td>1.122</td>
<td>1.317</td>
<td>1.069</td>
<td>1.091</td>
<td>0.957</td>
</tr>
<tr>
<td>2001–2002</td>
<td>311</td>
<td>0.996</td>
<td>0.990</td>
<td>0.971</td>
<td>0.937</td>
<td>1.100</td>
</tr>
<tr>
<td>2002–2003</td>
<td>311</td>
<td>0.918</td>
<td>1.000</td>
<td>0.879</td>
<td>1.000</td>
<td>0.969</td>
</tr>
<tr>
<td>2003–2004</td>
<td>288</td>
<td>0.928</td>
<td>0.876</td>
<td>0.863</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>2004–2005</td>
<td>279</td>
<td>1.000</td>
<td>1.086</td>
<td>1.000</td>
<td>0.857</td>
<td>1.031</td>
</tr>
<tr>
<td>2005–2006</td>
<td>282</td>
<td>0.903</td>
<td>0.829</td>
<td>0.907</td>
<td>0.941</td>
<td>1.000</td>
</tr>
<tr>
<td>2006–2007</td>
<td>280</td>
<td>1.012</td>
<td>1.073</td>
<td>0.890</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>2007–2008</td>
<td>302</td>
<td>0.996</td>
<td>1.040</td>
<td>0.963</td>
<td>1.001</td>
<td>0.969</td>
</tr>
<tr>
<td>2008–2009</td>
<td>283</td>
<td>0.851</td>
<td>0.895</td>
<td>0.866</td>
<td>1.000</td>
<td>0.717</td>
</tr>
<tr>
<td>2009–2010</td>
<td>247</td>
<td>1.008</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
</tr>
</tbody>
</table>

Growth from the small to medium size class had a transition probability of 21.4%, while growth from the medium to large size class had an only an 8.5% transition probability. Retrospection from the medium to small size class was rare, with a 3.3% transition probability. However, retrospection from the large to medium size class had a 25.3% transition probability. Fecundity values were slightly higher for large (0.129) than for medium (0.104) cacti. Annual survival probabilities (growth + stasis) increased from the small to large size classes (small = 0.86; medium = 0.92; large = 0.93).

Population growth rates (λ) for the pooled annual transition matrices (Table 1) indicated negative (λ < 1) population growth from 1988 to 1991, positive (λ > 1) population growth from 1992 to 2002, and variable population growth from 2003 to 2010, with 4 yr of positive or near-positive growth rates (2004, 2006–2008, 2009), and 4 yr of negative growth rates (2002–2004, 2005, 2008). The λ values ranged from a low of 0.72 during the 1989–1990 census to a high of 1.27 from 1992 to 1993. For the overall pooled transition matrix (all plots and years), λ was 0.982, indicating a slightly decreasing population (Table 2).

For individual plots, λ values from pooled transition matrices showed decreasing populations in all but the Badger Creek plot, where λ was positive (1.023, Table 2). North Canyon East had the lowest λ of 0.92. The pooled transition matrix for Badger Creek showed the highest fecundities for medium- and large-sized cacti, along with the second-highest survival rates for these size classes, explaining the high λ. Although North Canyon East had the second highest survival rates, this plot also had the lowest survival rates for cacti across all size classes, resulting in the lowest λ. Soap Creek had the highest survival for medium and large cacti, but the lowest fecundity values of any plot, which also resulted in a low λ (0.974). Of the individual vital rates, stasis of large-sized cacti and shrinkage from large to medium size classes had the largest standard deviations between plots (0.153 and 0.144, respectively), followed by fecundity.
of large-sized cacti (0.140). Annual transition probabilities for all plots are provided in Appendix S3.

Stochastic population growth rates ($\lambda_s$) for pooled transition matrices were lower than deterministic growth rates ($\lambda$) in all cases (Table 2). $\lambda_s$ for the overall pooled transition matrix (0.961) again indicated a declining population, with a 95% confidence interval of 0.959–0.962. For individual plots, Badger Creek had the highest $\lambda_s$ value at 1.008, while North Canyon East had the lowest $\lambda_s$ at 0.860. Both the North Canyon East and West plots had $\lambda_s$ values substantially lower than $\lambda$, likely due to the extremely low population growth rates from 1989 to 2008.

**Elasticity and life table response experiments**—Elasticity analysis for the overall pooled transition matrix (Table 3) showed that stasis had a much higher overall elasticity (0.757) than either growth (0.127) or fecundity (0.070). Stasis of medium-sized cacti had an elasticity (0.493) over 30% larger than either growth (0.127) or fecundity (0.070). Stasis showed the largest contributions to $\lambda$ in years with stable (0.99 < $\lambda$ < 1.01) or positive population growth, but caused decreases in $\lambda$ during years with negative population growth.

**Climate and hierarchical partitioning**—Total precipitation ranged from a low of 91 mm during the 1988–1990 census to a high of 366 mm during the 1994–1995 census period (Fig. 2). The 2 yr with lowest annual precipitation, 1989 and 2008, also corresponded to the years with the lowest $\lambda$ values for pooled transition matrices ($\lambda = 0.722, 0.851$, respectively; Table 1). In 1989, maximum summer temperatures were also above the long-term average, though they approximated the long-term average in 2008 (Fig. 2). Summer maximum temperatures were highest during the 2002–2003 and 2003–2004 census periods, when $\lambda$ values for the pooled transition matrix were again low ($\lambda = 0.918, 0.928$, respectively; Table 1). Winter minimum temperatures were lowest from 1990 to 1991 and from 2005 to 2006 (~4.85, −3.45°C, respectively; Fig. 2), corresponding to years with the second and fourth lowest population growth ($\lambda = 0.760, 0.903$, respectively). Winter minimum temperatures were highest from 1996 to 1997 (0.08°C), a year of positive population growth ($\lambda = 1.075$). Spring maximum temperatures ranged from a low of 20.38°C in 1991 to a high of 30.11°C in 1995 (Fig. 2).

Among the eight climate variables we derived, only annual precipitation, 2-yr average annual precipitation, and winter minimum temperature showed significant independent contributions in the HP models (Table 4). Annual precipitation was significant in HP models for both $\lambda$ and mortality, while the 2-yr average precipitation was significant in the HP model for $\lambda$. Winter minimum temperature was also significant in the HP model for $\lambda$. A linear regression of the relationship between annual precipitation and $\lambda$ gave an R$^2$ value of 0.27 ($F_{1,20} = 8.75, P = 0.007$; Fig. 3), while the linear regression between annual precipitation and annual mortality gave an R$^2$ of 0.12 and was only marginally significant ($F_{1,20} = 3.79, P = 0.06$; Fig. 3).
Both deterministic and stochastic population growth rates indicated that populations of P. bradyi may decline in the future, depending on relationships between demographic processes, climate, and other stochastic events. The southwestern United States is predicted to become hotter and drier, with an increased frequency of both drought and extreme precipitation events (IPCC, 2013). Stochastic simulations based on these predictions indicated that populations of P. bradyi may not be resilient to such changes in climate over the long term. The negative effects of an increased frequency of drought could be partially mitigated by a concomitant increase in extreme precipitation, but λs still declined under such a scenario in our analysis. This finding contrasts with predictions of increased population growth resulting from projected climatic changes for more common desert species (Salguero-Gómez et al., 2012). Apparently, possible physiological mechanisms for coping with harsh climatic conditions found in P. bradyi, including high transition linear regression between 2 yr annual precipitation and λ gave an $R^2$ of 0.23 ($F_{1,20} = 7.45, P = 0.01$; Fig. 3). Finally, the linear regression between λ and winter minimum temperature gave an $R^2$ of 0.15 ($F_{1,20} = 4.69, P = 0.04$; Fig. 3).

**Stochastic simulations and quasi-extinction risk**—Simulations representing the two climate change scenarios affected λs differently. Increasing the probability of drought alone (represented by the 1989–1990 and 2008–2009 pooled transition matrices) decreased λs in all simulations (Fig. 4). These reductions were approximately linear, with λs falling from 0.958 at the $1.25\times$ probability level to 0.940 at the $3\times$ probability level. Simulations with increased probabilities for both drought and extreme precipitation (represented by the 1992–1993 and 2004–2005 pooled transition matrices) also reduced λs, but less so, with estimates falling from 0.959 at the $1.25\times$ probability level to 0.956 at the $3\times$ probability level (Fig. 4).

Quasi-extinction risks for P. bradyi increased with an increasing probability of drought (Fig. 5). For the equal probabilities simulation, representing observed conditions, the probability of a population size <10 after 75 yr dropped below 0.5 with an initial population size of approximately 250 cacti. However, a quasi-extinction probability <0.5 would require initial population sizes of approximately 325, 475, 650, and 950 cacti for the $1.5\times$, $2\times$, $2.5\times$, and $3\times$ probability levels, respectively.

**Variability in estimates of λ**—Estimates of λs varied greatly based on the length of the monitoring period, as indicated by the gradual reduction in the lengths of error bars as the number of consecutive years included in simulations increased (Fig. 6). The mean and standard deviation of the distribution of λs values from randomly sampled, 2-consecutive-year census periods were 0.963 ± 0.082, while these estimates for the 18-consecutive-year census periods were 0.978 ± 0.012, indicating a large reduction in the degree of uncertainty surrounding λs estimates. Standard deviations of λs distributions fell on both sides of the unity value ($\lambda_s = 1$)—indicating that the population could have been projected as either increasing or decreasing—until the duration of monitoring reached 14 yr.
Quasi-extinction risks based on the scenario of increased drought suggested that from several hundred to a thousand cacti would be required for populations to remain viable after 75 yr (Fig. 5). From a management perspective, this finding is important because no reliable estimate of the total population size of *P. bradyi* exists, although over 500 cacti are likely present across all monitoring plots. The species is thought to be restricted to a particular soil type (L. Hughes, personal observation; USFWS, 1985), but an estimate of the size of existing suitable habitat as well as the conservation status of these lands is not yet available. This information would provide a far better context within which to interpret our calculations of stochastic growth rate and quasi-extinction risk.

Elasticity analyses for *P. bradyi* were largely consistent with demographic research conducted on other members of the Cactaceae (Valverde et al., 2004; Valverde and Zavala-Hurtado, 2006; Jiménez-Sierra et al., 2007; Martínez et al., 2010), particularly our finding that elasticity values for stasis were highest, while those for fecundity were lowest—a pattern that is common for long-lived species (Silvertown et al., 1996). However, when years of positive population growth were contrasted with years of decline in an LTRE, both fecundity (a 1 in Fig. 1) and stasis (a 22 in Fig. 1) of medium-sized cacti had the largest influences on population growth. Similar results were obtained in probabilities for shrinkage (Salguero-Gómez and Casper, 2010) and the ability to retract below ground (Garrett et al., 2010), may not be enough to buffer against changes in the frequency or intensity of extreme climatic events.

### Table 4

<table>
<thead>
<tr>
<th>Environmental variable</th>
<th>1 yr</th>
<th>2 yr</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual precipitation</td>
<td>0.22</td>
<td>0.15</td>
</tr>
<tr>
<td>Winter min temperature</td>
<td>0.15</td>
<td>0.11</td>
</tr>
<tr>
<td>Summer max temperature</td>
<td>0.05</td>
<td>0.03</td>
</tr>
<tr>
<td>Spring max temperature</td>
<td>0.00</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Notes: max = maximum, min = minimum.

Fig. 3. Change in population growth (λ) and annual mortality for *Pediocactus bradyi* in relation to annual precipitation, 2-yr average precipitation, and winter minimum temperature. Solid lines show the linear regressions between climatic variables (x-axes) and λ (y-axes on left panels) or the logarithm of annual mortality (y-axis, right panel).
comparisons among species of *Neobuxbaumia* with differing degrees of rarity (Esparza-Olguín et al., 2005), highlighting how elasticity values tend to be correlated with $\lambda$; stable or declining populations have higher values for stasis, while growing populations have higher values for fecundity (Silvertown et al., 1996). Desert species with episodic recruitment will likely have different elasticity values depending upon conditions encountered during monitoring. By explicitly accounting for this, our LTRE showed fecundity to be as important as stasis in shaping the long-term population growth of *P. bradyi*. This relationship was also apparent in comparisons across plots, as both the North Canyon East and Soap Creek plots had low $\lambda$, but for opposite reasons: low survival was coupled with high fecundity at North Canyon East, while high survival was coupled with low fecundity at Soap Creek (Table 2).

Population growth was correlated with both increased annual precipitation and higher winter minimum temperatures in regression models. Given the LTRE analysis, it is likely that survival and fecundity were the demographic processes most influenced by these climatic factors. Extreme low temperatures can be fatal for cacti, although species differ in cold temperature tolerance (Nobel, 1988; Drezner and Lazarus, 2008). However, winter minimum temperature was significantly correlated with $\lambda$, but not mortality, in HP models, suggesting an influence on regeneration rather than survival. Annual precipitation, on the other hand, influenced both demographic processes. Mortality was highest following years with low precipitation, particularly the two census periods with the lowest recorded precipitation during our study (1989–1990, 2008–2009; Fig. 2), which also represented drought in our stochastic simulations. Importantly, the vast majority of the mortalities that occurred during these periods resulted from increased rodent herbivory rather than desiccation. Indeed, 85 rodent-caused mortalities were recorded following the 1989–1990 census and 35 after the 2008–2009, the highest levels encountered in our study (Appendix S3). During these periods, rodents likely turned to *P. bradyi* for nourishment due to a lack of other food sources. Such interactions are common in arid environments, both for cacti (Hoffman et al., 1993; Hayes et al., 2013) and other species (Ticktin, 2003; Holmgren et al., 2006), and may heighten the impacts of drought through synergy among trophic levels (DeFalco et al., 2010). A well-known example is the widespread die-off of piñon pines (*Pinus edulis*) following severe droughts from 2002 to 2003, caused by bark beetle infestations of drought-weakened trees (Breshears et al., 2005). Understanding how such biotic interactions—mediated by climatic conditions—shape demographic processes will be essential in predicting the responses of species to climate change.

Precipitation is thought to be the most limiting factor for cactus regeneration (Godínez-Alvarez et al., 2003). Because cacti do not establish persistent seedbanks, seedling establishment for species without vegetative reproduction (most columnar, barrel, and globose cacti) generally peaks following rare, heavy precipitation events (Drezner and Lazarus, 2008). This pattern appears to hold for *P. bradyi*, which established a large seedling cohort following an El Niño driven precipitation pulse in 1992 (Fig. 2). However, after adequate precipitation enables germination, seedling establishment may depend on a hierarchy of other factors, notably temperature. For example, high summer temperatures can decrease seedling survival (Drezner, 2004), while high winter temperatures may increase survival (Drezner et al., 2011).
tions are neither growing nor declining.

Horizontal dashed line indicates the point of stability (\( \lambda_s = 1 \)) until the monitoring period reached a length of 14 yr (Fig. 6). Uncertainty in shorter-term projections and did not converge upon a consistent estimate of \( \lambda_s \) for the long-term population growth of \( P. bradyi \) and Lazarus, 2008). The regeneration peak for \( P. bradyi \) in 1992 was accompanied by both below-average summer and above-average winter temperatures (Fig. 2). However, conditions may have been less favorable following heavy precipitation in 2004, when summer temperatures were above average and \( P. bradyi \) did not establish a seedling cohort. Further research is needed to understand how interactions between changing precipitation and temperature regimes will affect regeneration ability for desert species, many of which have narrow climatic requirements for successful recruitment (Meyer and Pendleton, 2005; Reynolds et al., 2012). Here, we have shown that fecundity was at least as important as survival in shaping the long-term population growth of \( P. bradyi \).

Our results also highlight the importance of basing assessments of population trends on long-term demographic data. Stochastic growth rates calculated for \( P. bradyi \) varied widely based on the length of the monitoring period included in simulations and did not converge upon a consistent estimate of \( \lambda_s \) as above or below unity (\( \lambda_s = 1 \)) until the monitoring period reached a length of 14 yr (Fig. 6). Uncertainty in shorter-term estimates of \( \lambda_s \) resulted from high spatiotemporal variability in population growth related to climate and biotic interactions. For example, during the drought from 1989 to 1990, both the North Canyon East and West plots were decimated by rodent herbivory, while the Badger and Soap creek plots were largely unaffected and had stable \( \lambda_s \) values (Table 1). This one event likely accounted for large part of differences in stochastic growth rates between plots (Table 2). Hard-to-predict stochastic events shape the long-term population trajectory of many desert species (Miriti et al., 2007), complicating efforts to model long-term population trends where only short-term information is available. Supporting previous treatments of this issue (Fieberg and Ellner, 2001; Doak et al., 2005), our results suggest that

long-term demographic data from multiple populations is necessary for accurate estimates of \( \lambda_s \).

**Conclusions**—Our study contributes a notable example of a rare desert species that may be susceptible to a changing climate. By linking long-term demographic data with trends from historical and projected future climates, we show that populations of \( P. bradyi \) may decline in response to an increased frequency or intensity of drought, even with a concomitant increase in extreme precipitation. Decreased population growth was related to climatic influences on multiple demographic processes, particularly fecundity and survival. Additionally, we find that consistent estimates of \( \lambda_s \) could only be derived through simulations including long-term demographic data. Our results support the use of demographic models to predict species’ responses to climate change, so long as there is adequate temporal replication of data.

**LITERATURE CITED**


