

# **Appendix from M. E. K. Evans et al., “Bet Hedging via Seed Banking in Desert Evening Primroses (*Oenothera*, Onagraceae): Demographic Evidence from Natural Populations”**

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## **Additional Methodological Details**

This appendix provides additional methodological details not found in the text. The structure follows that of the “Methods” section (“Species and Sites,” “Plant Demography,” “Seed Demography,” “Population Models,” “Testing Predictions of Bet Hedging”), followed by two sections not identified separately in the text: “Generating Confidence Intervals for Growth Rates” and “Temporal Autocorrelation in Precipitation.” The section on confidence intervals is subdivided into descriptions of the methods for deterministic single-year growth rates ( $\lambda$ ), long-run stochastic growth rates ( $\lambda_s$ ), average environment growth rates ( $\lambda_a$ ), and variation in single-year growth rates ( $\text{Var}(\lambda)$ ).

## **Species and Sites**

The two species used in this study are very closely related: they were formerly subspecies of the same species (Klein 1962, 1964, 1970; Wagner 1993, 1998; Evans et al. 2005). Both occur in scattered populations in the loose, coarse-grained (sandy or gravelly) soils associated with drainages (washes, rivers) or roadsides (Klein 1970). Both are winter recruiting. Germination typically occurs in response to rainfall of  $\geq 25$  mm in the autumn (as described by Beatley [1974]). Individuals of *Oenothera californica* ssp. *avita* (the perennial) may survive through the summer, typically with little or no living aboveground biomass. Surviving plants can sprout from the base or produce rosettes from underground horizontal rhizomes either in the summer (if summer rain is sufficient, in which case a second bout of flowering may occur in some individuals) or in the following season of seedling recruitment.

We censused survival and fertility in three naturally occurring populations of *O. californica* ssp. *avita* (hereafter, the perennial) and in two populations of *Oenothera arizonica* (hereafter, the annual). The study populations of the perennial are designated, in order of increasing elevation, the Private (1,150 m; 35°15'N, 113°40'W), State (1,210 m; 35°15'N, 113°40'W), and BLM (1,300 m; 35°01'N, 113°49'W) sites (near Kingman, AZ). The study populations of the annual are designated the Buckeye (270 m; 33°20'N, 112°38'W) and Hassayampa (300 m; 33°29'N, 112°45'W) sites (near Phoenix, AZ). Cumulative precipitation in the 4 years of the study, as well as average precipitation, is shown in figure A1, using records from three weather sources near the study sites.

## **Plant Demography**

While collecting data in the perennial populations, we distinguished three types of plants: seedlings, adults, and clones. Seedlings were identified by the presence of distinctively shaped cotyledons, which typically remained detectable over the census interval of 8 weeks. (Data from perennial populations in the first year of the study, 1999–2000, are not shown because of initial difficulty identifying seedlings.) Clonal rosettes (clones) sprouted from roots belowground, so they could not be grouped into genets. Hence, we treated clones on a ramet basis; that is, we collected separate survival and fecundity data for each ramet. A ramet typically included just one clonal rosette, but clonal rosettes that were tightly clustered were treated as a single ramet. Adults included plants that had been identified as seedlings that survived to produce at least one fruit and any time thereafter (i.e., resprouting from the base rather than spreading via clonal rosettes). We recorded data from as many plants as possible at each study site in 1 day (see sample sizes in table 1), resulting in five sampling days every 8

weeks over a 4-year period. Plants that had died were frequently relocated rather than being determined dead by their absence.

Seed output was estimated after the end of the flowering season. We counted the number of fruits on every plant in census areas. Fruits were collected from a subset of these plants, and the number of seeds per fruit was counted using a dissection microscope. Seed output per plant was estimated by multiplying the number of fruits per plant by the mean number of seeds per fruit for a given population and year. We did not quantify seed output in response to summer rain in the perennial populations, which involved very few individuals.

## Seed Demography

We estimated germination fraction and soil seed survival from data on the density of viable, ungerminated seeds in the soil. Soil samples were collected after germination had ended but before new seeds were dispersed, using a  $7 \times 4.5$ -cm (diameter  $\times$  depth) soil tin, in the spring of the years 2001–2003. Soil samples ( $N = 46$ –68/year) were collected in a spatially stratified random manner at each study site. We used the flotation method described by Pake and Venable (1996) to sort seeds from soil samples. The viability of seeds was assessed by visual criteria and by dissection when necessary. The census interval of 8 weeks was short enough that we occasionally detected seedlings that had emerged and died between censuses. That we did detect dead seedlings suggests that seedling mortality and seed bank mortality were minimally confounded in this data set.

We calculated survival of seeds in the soil based on these estimates of soil seed density, together with estimates of seed rain and seedling density (table A1). Seed rain and seedling density were the estimated total number of seeds produced and seedlings that emerged in census areas in a given season, respectively, divided by that area. The density of ungerminated, viable seeds from one year to the next ( $S_{(t-1)}$  and  $S_{(t)}$ , respectively) changes according to the equation

$$S_{(t)} = [(S_{(t-1)} \times s_{p(t-1)} + G_{(t-1)}) \times s_{s(t-1)} - L_{(t)}] \times s_{w(t)},$$

where  $G_{(t-1)}$  and  $L_{(t)}$  are estimates of seed rain density and seedling density, respectively, the gains and losses to soil seed density. Seed survival in three intervals enters into this equation: from the time of soil seed sampling to the time of seed rain ( $s_p$ ), from the time of seed rain to the time of germination ( $s_s$ ), and from the time of germination to soil seed sampling ( $s_w$ ). We define the time of germination as the census date by which at least half of the total observed seedlings had been recorded.

To solve the equation for the seasonal seed bank survival rates,  $s_p$ ,  $s_s$ , and  $s_w$ , we assume a constant rate of seed survival (i.e., an exponential decay model, as discussed in Crawley 1996; Silvertown and Charlesworth 2001). Then any two of the survival rates can be expressed as a function of the third, according to the number of days in each of the three intervals (see table A1). The equation is solved (numerically) for one unknown (one seed survival parameter), and the remaining two seed survival parameters are calculated from that. The underlying rate of seed survival for each population in each year is reported in table A1, expressed as a rate per 365 days.

In the annual populations, soil seed sampling and plant censuses were conducted at the same point in time, so the number of days between the two is 0 and  $s_p = 1.0$ . Fruits were mature but had not opened to disperse seeds. In the perennial populations, soil sampling occurred approximately 40–50 days before plant censusing. Thus, the estimate of  $s_p$  based on the 2001–2002 soil seed data is not the correct estimate for use in the 2001–2002 population projection. Instead, the estimate of  $s_p$  based on the 2002–2003 soil seed data is the correct value to use. This also means that there is missing information on  $s_p$  at the end of the data series; another soil sample in 2004 would be required to estimate  $s_p$  for the 2002–2003 transition matrix. To fill in this missing estimate of  $s_p$ , we assume that soil seed survival continues at the underlying rate estimated on the basis of the 2002–2003 soil seed data and find  $s_p$  according to the number of days between the last soil sample and the last plant census.

## Population Models

### *Annual Populations*

The finite rate of increase,  $\lambda$ , of the annual populations, is given by a scalar model

$$\lambda = \frac{S_{(t)}}{S_{(t-1)}} = [s_s \times (1 - g) \times s_w \times s_p] + (s_s \times g \times s_j \times F_a),$$

where  $S_{(t)}$  is the number of seeds immediately after reproduction in year  $t$ ,  $s_s$ ,  $s_w$ , and  $s_p$  are the rates of seed survival in three intervals per year (as described above),  $g$  is the fraction of seeds that germinate,  $s_j$  is the fraction of seedlings that survive to produce at least one fruit, and  $F_a$  is the mean number of seeds produced by plants that make at least one fruit (see fig. 1a). The first term on the right-hand side of this expression quantifies the fitness achieved by dormant seeds in the soil seed bank, whereas the second term quantifies the fitness achieved by seeds that germinate.

### Perennial Populations

The perennial populations are modeled with three life stages: seeds, adults, and clones. We did not distinguish between first-year adults (seedlings that survived to reproduce) and adults after their first year. We did not see obvious differences in their fertility, and the sample sizes in the two groups were badly unbalanced (no first-year adults in 2001–2002 and very few adults after their first year in 2002–2003; table 1); a test of fecundity differences would be compromised by this aspect of data. The dynamics of the perennial populations are governed by the equation

$$\mathbf{n}_{(t+1)} = \mathbf{A}_{(t)} \times \mathbf{n}_{(t)}$$

where  $\mathbf{n}$  refers to a vector of the abundances of the three classes of individuals (seeds, adults, and clones) and  $\mathbf{A}$  refers to the transition matrix

$$\mathbf{A} = \begin{bmatrix} [s_s \times (1 - g) \times s_w \times s_p] + (s_s \times g \times s_j \times F_a) & s_a \times F_a + s_a \times C \times F_c & s_c \times F_c + s_c \times C \times F_c \\ s_s \times g \times s_j & s_a & 0 \\ 0 & s_a \times C & s_c + s_c \times C \end{bmatrix},$$

which follows from the life cycle diagram in figure 1b. The upper left element of the matrix contains the annual model (the seed-to-seed transition). In addition to the parameters in the annual model, there is a term describing the rate of adult survival ( $s_a$ ), a term describing mean seed production per clone ( $F_c$ ; the average among all clones whether they produced fruits or not), and two terms relating to clonal rosettes: clone survival ( $s_c$ ) and clone production ( $C$ ). The second element in the first row indicates that adults may give rise to seeds in the next time step both by surviving as an adult and reproducing as an adult ( $s_a \times F_a$ ) and, conditional on surviving, by producing clones and reproducing as a clone ( $s_a \times C \times F_c$ ). The third element in the first row indicates that clones may give rise to seeds in the next time step both by surviving as a clone and reproducing ( $s_c \times F_c$ ) and, conditional on survival, by producing new clones and reproducing ( $s_c \times C \times F_c$ ). The lower right element implies that in addition to surviving from one year to the next, conditional on survival, clones give rise to new clones (at the rate  $C$ ). Other elements are straightforward.

To find the rate of clone production, we use the following equation for clone dynamics (derived from the model above):

$$R_{(t)} = (s_a \times C) \times A_{(t-1)} + (s_c + s_c \times C) \times R_{(t-1)},$$

where  $R_{(t)}$  indicates the number of clones at time  $t$  (see table A2) and  $A_{(t)}$  the number of adults. By assuming that clone survival ( $s_c$ ) is equal to adult survival in the same population and year, the equation can be solved for  $C$ , the rate of clone production by adults and clones.

We constructed transition matrices for each pair of years of data from each perennial population. However, we pooled data on adult survival in the 2002–2003 year: very few adults survived the drought year 2001–2002, so the number of adults at the beginning of the 2002–2003 season (a wet year) was small. Thus, we used the unweighted average adult survival across all three perennial populations for the year 2002–2003 ( $1/12 = 0.083$ ) in all analyses.

The dominant eigenvalue of each transition matrix was estimated numerically by simulating population growth

for 100 time steps in Excel, as described by Donovan and Welden (2002). These simulations were initiated with a vector of 1,000 seeds, 100 adults, and 10 clones. Single-year growth rates converged (up to six decimal places) within 5–13 years.

## Testing Predictions of Bet Hedging

We test for the population dynamic patterns expected under bet hedging using stochastic simulations of population growth in ULM (Unified Life Models, ver. 4.0). We made one modification to the data before conducting these simulations: the reproductive success of the dry year was increased to a small nonzero value (see “Methods”). We chose a value for seedling survival ( $s_j$ ) that treats the observed zeros as sampling zeros: while all seedlings died without reproducing in sample areas in the dry year, the sample areas did not include the entire population. There may have been a small number of plants outside of sample areas that produced seed. The largest number of seedlings that we observed at one site (which all died without reproducing) was 255; hence, any nonzero rate of seedling survival would likely be smaller than  $1/255$  at that site; we chose the value 0.003 ( $1/333$ ). This is potentially conservative in the sense that the number of seedlings monitored was smaller at other sites (84 and seven seedlings tracked at the annual sites). We changed the 0 value for seed production of first-year adults to 25 seeds (2001–2002; note that the value for  $F_a$  in  $a_{12}$  remained 0), which is in the range of relatively small nonzero values that were observed (i.e., 24 seeds, State site, 2002–2003; table 1) and is less than what can be produced in a single fruit. Hence, the reproductive success of the dry year becomes  $0.003 \times 25 = 0.075$  seeds produced per germinated seed. This changed the single-year growth rates of the dry year by an amount on the order of or less than rounding error compared with the number of significant digits reported in table 2. For example, for the Hassayampa site, it changes the  $\lambda$  of the dry year from 0.044750 to 0.044757, and the value reported in table 2 is 0.04. We make this change consistently across all sites and analyses.

We used the years for which we have data for the entire life cycle (2001–2003), which yields two transitions: one of these years was dry (2001–2002) and one wet (2002–2003). Using long-term weather records as a guide to choose a probability of the wet year ( $p$ ) versus the dry year ( $1 - p$ ) proves to be problematic. For example, the weather station nearest the annual study sites (at Buckeye, AZ) recorded 4.42 cm of precipitation between September and May of the dry year (2001–2002) and 22.96 cm in the same period the following year, the wet year. The long-term average (among the years 1893–2003) of precipitation recorded in September–May at this weather station is 19.25 cm. The frequency of the wet year that leads to a weighted average of 19.25 cm is  $p = 0.74$ . The long-run stochastic growth rates of the Buckeye and Hassayampa populations, applying this value of  $p$ , are 1.97 and 12.27, respectively, well above the replacement value of 1.0. Hence, this seems like an inappropriate value for the frequency of the wet versus the dry years. The long-run stochastic growth rates obtained for the perennial study sites, using the same procedure and data from the nearest weather station, are also too large. This is probably because the wet year is not much greater than the long-term average, whereas the dry year is exceptionally dry, so achieving the long-term average requires an unrealistically high frequency of the wet year. Hence, we explore the entire range of the frequency of the wet year ( $p$ ).

To estimate long-run stochastic growth rates, we ran Markov chain Monte Carlo simulations of population growth in ULM, version 4.0. In these simulations, a Bernoulli trial selects either the vital rates from the wet year (probability  $p$ ) or the vital rates from the dry year (probability  $1 - p$ ) at each time step. In the case of the annual populations, one of the two single-year  $\lambda$ 's (2001–2002 vs. 2002–2003) is multiplied by the current population size (the number of seeds), projecting the population forward one time step. In the case of the perennial populations, one of two transition matrices (2001–2002 vs. 2002–2003) is multiplied by the current vector of abundances of seeds, adults, and clones, projecting the population forward one time step. Simulations were initiated with one seed.

We ran batch files of these simulations of population growth, increasing the number of time steps, in order to examine the convergence dynamics of the long-run stochastic growth rate (with and without seed banks). We varied the number of time steps from 2,000 to 200,000. We chose a number of time steps (5,000) by which the fluctuations in the long-run stochastic growth rate had stabilized; that is, further increase in the length of the simulation did not reduce variation in the long-run stochastic growth rate. For the test of bet hedging, we ran simulations of 6,000 time steps: 5,000 to reach convergence and another 1,000 to sample the one-time-step growth rates after convergence. In order to run long simulations across the full range of  $p$  (including both rapidly growing and rapidly shrinking populations), we normalized the population to sum to 1 at each time step. We

calculated the long-run stochastic mean growth rate as the arithmetic average of the log of 1,000 one-time-step growth rates, after convergence (as in eq. [14.16] in Caswell 2001):

$$\exp \left\{ \frac{\sum \ln [P_t/P_{(t-1)}]}{1,000} \right\},$$

where  $P$  is total population size (the number of seeds in annual populations vs. the sum of seeds, adults, and clones in perennial populations). Using the same frequency of the two transitions (year types), long-run stochastic growth rates were recalculated after eliminating seed banking (setting germination fraction to 1.0).

We calculated average environment growth rates ( $\lambda_s$ ) with and without seed banks across the full range of frequencies of the wet versus the dry year. For the annual populations, the average environment growth rate is the average of the two single-year  $\lambda$ 's (2001–2002 and 2002–2003), weighted by their frequency. For the perennial populations, the average environment growth rate is the dominant eigenvalue of the weighted mean projection matrix, where each matrix element is the weighted mean of that element in the wet versus the dry year, weighted by their frequency. This dominant eigenvalue was estimated numerically (by simulating population growth for 100 time steps in Excel, which was more than sufficient to reach convergence) as described above. We then recalculated average environment growth rates, after eliminating the seed bank by setting germination fraction to 1.

We quantified fitness variation in terms of the variance among one-time-step growth rates in the last 1,000 time steps of the stochastic simulations of population growth with and without seed banks described above (i.e., where  $\lambda_s$  is estimated).

## Generating Confidence Intervals for Growth Rates

Confidence limits were calculated for the long-run stochastic and average environment growth rates, with and without seed banking, using a baseline value of  $p$ . In the three populations with  $\lambda < 1$  in the dry year and  $\lambda > 1$  in the wet year (Buckeye, Hassayampa, State), this baseline value is the probability of the wet year ( $p^*$ ) that leads to a long-run stochastic growth rate of 1.00. At the BLM site,  $\lambda > 1$  in both years but more so in the wet year (table 2), so we attempt to minimize  $\lambda_s$  by using a low value of  $p$ . At the Private site,  $\lambda < 1$  in both years but more so in the wet year, so we attempt to maximize  $\lambda_s$  by choosing a low value of  $p$ . For these two populations, we use  $p = 0.1$ . This value is arbitrary, but these two populations fail to show expected bet-hedging patterns regardless of the value of  $p$ , so the choice is inconsequential (fig. 3).

Confidence intervals for population growth rates are typically constructed using bootstrapping methods (Kalisz and McPeck 1993; Caswell 2001; Morris and Doak 2002). Some of our estimates of vital rates, like seedling survival, adult survival, and fecundity of adults and clones, come from plants that could be identified and relocated over time; these data can be resampled (i.e., nonparametric bootstrapping). Estimates of other vital rates, such as germination fraction, survival of seeds in the soil, and clone production, come from balancing dynamical equations (of seeds and clones, respectively) at the level of populations. Nonetheless, we wish to reflect the variability and uncertainty associated with these vital rates. To do so, we assume that the estimates were drawn from appropriate distributions: in the case of germination fractions and seed survival (which can vary from 0 to 1), we assume they are drawn from beta distributions. The beta distribution is appropriate because it allows us to choose an expected value between 0 and 1 and model uncertainty via the variance of the distribution. Further details follow. The 95% confidence intervals (calculated using the bias-corrected percentile method) for each vital rate are shown in table A3.

We describe our method of constructing confidence intervals for deterministic single-year growth rates first, followed by the method for long-run stochastic and average environment growth rates. All that follows was accomplished in R; this code is available by request from M.J.K.

### *Deterministic Single-Year Growth Rates*

*Annual populations.* In the annual model,  $s_j$  and  $F_a$  occur as a product in only one place in the equation governing annual population growth; hence, we can model their product. The product of  $s_j$  and  $F_a$  in the wet year is the only parameter for which we have individual-level data that can be resampled; we sample randomly

from the data (with replacement), until we have a new data set equal in size to the field sample, and find the mean of that sample. As described in the footnote to table 2 and above, we replaced the 0 values for  $s_j$  and  $F_a$  in the dry year with 0.003 and 25, respectively.

We model the remaining parameters ( $g$ ,  $s_s$ ,  $s_w$ ) as stochastic realizations drawn from beta distributions. We model germination in the dry year and germination in the wet year as two different distributions, reflecting the tendency for little germination when there is little precipitation (i.e., adaptive plasticity in germination behavior). We use maximum likelihood methods to estimate these beta distributions from the germination fractions reported in table 1, irrespective of species. In growth chamber experiments, seeds of the annual tended to germinate at a lower rate than seeds of the perennial, but this difference was not significant (Evans 2003), giving us justification for treating the estimates of germination fraction from both species as draws from a single distribution. The maximum likelihood estimates of the shape parameters for these beta distributions are 1.1341 and 4.453 (germination in the wet year) and 0.047 and 3.018 (germination in the dry year).

Given the lack of consistent differences in soil seed survival according to year type or species, we model the estimates of annual and perennial soil seed survival in the dry and the wet year as stochastic draws from a single (beta) distribution. We use maximum likelihood methods to estimate this beta distribution of soil seed survival (per 365 days) from the values reported in table A1 (excluding the value 1.0), yielding the shape parameters 0.734 and 3.830. Once a random value is drawn from this beta distribution, we convert to the appropriate time interval using the number of days in  $s_s$  and  $s_w$  reported in table A1.

A set of 1,000 growth rates ( $\lambda$ 's) for the dry and the wet year (each) were generated by entering new vital rates into the equation governing population dynamics (see “Population Models,” above). We then substituted  $g = 1.0$  into these same 1,000 combinations of vital rates and recalculated  $\lambda$ , generating corresponding distributions of  $\lambda$  in the wet versus the dry year without seed banks. Hence, each bootstrapped value of  $\lambda$  has a sister value without the seed bank. These  $\lambda$ 's were stored for later use, and 95% confidence intervals were computed for each population and year type (with and without seed banks) using the bias-corrected percentile method described by Caswell (2001).

*Perennial populations.* The perennial model has 10 parameters. Germination fraction ( $g$ ) and soil seed survival ( $s_s$ ,  $s_w$ , and  $s_p$ ) were modeled as described above in the annual model, although in the perennial model  $s_p \neq 1.0$  (see “Population Models,” above). In the perennial model,  $s_j$  and  $F_a$  cannot be modeled as a product because they do not always occur together (see  $a_{12}$  and  $a_{21}$ ). A random sample (with replacement) was taken from the data from the wet year for each ( $s_j$ ,  $F_a$ ) to build new data sets equal in size to the field samples, and the mean of each new sample was calculated. As above, we replaced the 0 values for seedling survival ( $s_j$ ) and seed production by first-year adults ( $F_a$ ) in the dry year with 0.003 and 25, respectively. Note, however, that the value for  $F_a$  in  $a_{12}$  in the dry year remained 0. Two additional parameters, unique to the perennial model, came from individual-level data, and those data were resampled with replacement to generate new values as described for  $s_j$  and  $F_a$ : adult survival ( $s_a$ ) and seed production per clone ( $F_c$ ). We modeled clone production ( $C$ ) as a negative exponential distribution by using maximum likelihood methods to estimate the shape parameter of this distribution (0.170), given the values reported in table 1. The negative exponential varies from 0 to infinity, with decreasing probability at higher values. The remaining parameter,  $s_c$ , the rate of clone survival, we set equal to the resampled value of adult survival ( $s_a$ ; as elsewhere).

Resampled vital rates were used to construct 1,000 new realizations of the transition matrix for each population in the dry versus the wet year, and the dominant eigenvalue of each matrix was computed analytically (using the eigen function in R). We then substituted  $g = 1.0$  into these matrices (eliminating the seed bank) and recalculated the dominant eigenvalues. The matrices were stored for later use, and 95% confidence intervals for the dominant eigenvalues were computed (per population and year type) by the bias-corrected percentile method.

### *Long-Run Stochastic Growth Rates*

To generate confidence intervals for long-run stochastic growth rates, we performed stochastic simulations of population growth identical to that described above but using the bootstrapped  $\lambda$ 's or matrices generated while constructing confidence intervals for single-year growth rates. A single stochastic simulation used just one pair of  $\lambda$ 's or matrices (wet vs. dry) for 6,000 time steps. At each time step, a Bernoulli process determined whether the population experiences a dry or a wet year (using the probability of the wet year  $p^*$  reported in table 2), and the population was projected one time step forward. The long-run stochastic growth rate was calculated from the last 1,000 time steps of simulations of 6,000 time steps, as described above. This was repeated 1,000 times, using all

of the bootstrapped  $\lambda$ 's or matrices (sequentially), generating 1,000 realizations of the long-run stochastic growth rate. We then repeated the process, using the same  $\lambda$ 's (annual populations) or matrices (perennial populations) but using the corresponding values without seed banks. This generated stochastic growth rates with and without seed banks ( $N = 1,000$  each). Confidence intervals (95%) were generated from these growth rates using the bias-corrected percentile method.

#### *Average Environment Growth Rates*

For annual populations, average environment growth rates were calculated by taking the weighted mean of pairs of  $\lambda$ 's, one bootstrapped  $\lambda$  from the wet year and one bootstrapped  $\lambda$  from the dry year. These bootstrapped  $\lambda$ 's had been stored in vectors; we computed the weighted mean of the first elements of these two vectors, followed by the weighted mean of the second elements, and so on, up to 1,000. The  $\lambda$ 's from the wet year were weighted by the value of  $p$ , the probability of the wet year, reported in table 2 for each population. This process was repeated for the corresponding  $\lambda$ 's without a seed bank ( $g = 1.0$ ), and 95% confidence intervals were generated for each class of average environment growth rates (each population with vs. without seed bank) using the bias-corrected percentile method.

The process was similar for the perennial populations except that we found the weighted mean of pairs of bootstrapped matrices (one wet year and one dry year) and then found the dominant eigenvalue for that weighted mean matrix (the weight of the wet year matrix is the value of  $p^*$  reported in table 2). This was repeated using corresponding matrices without seed banks ( $g = 1.0$ ). Confidence intervals (95%) were calculated for average environment growth rates for each population, with and without seed banking, by the bias-corrected percentile method.

#### *Variation in $\lambda$*

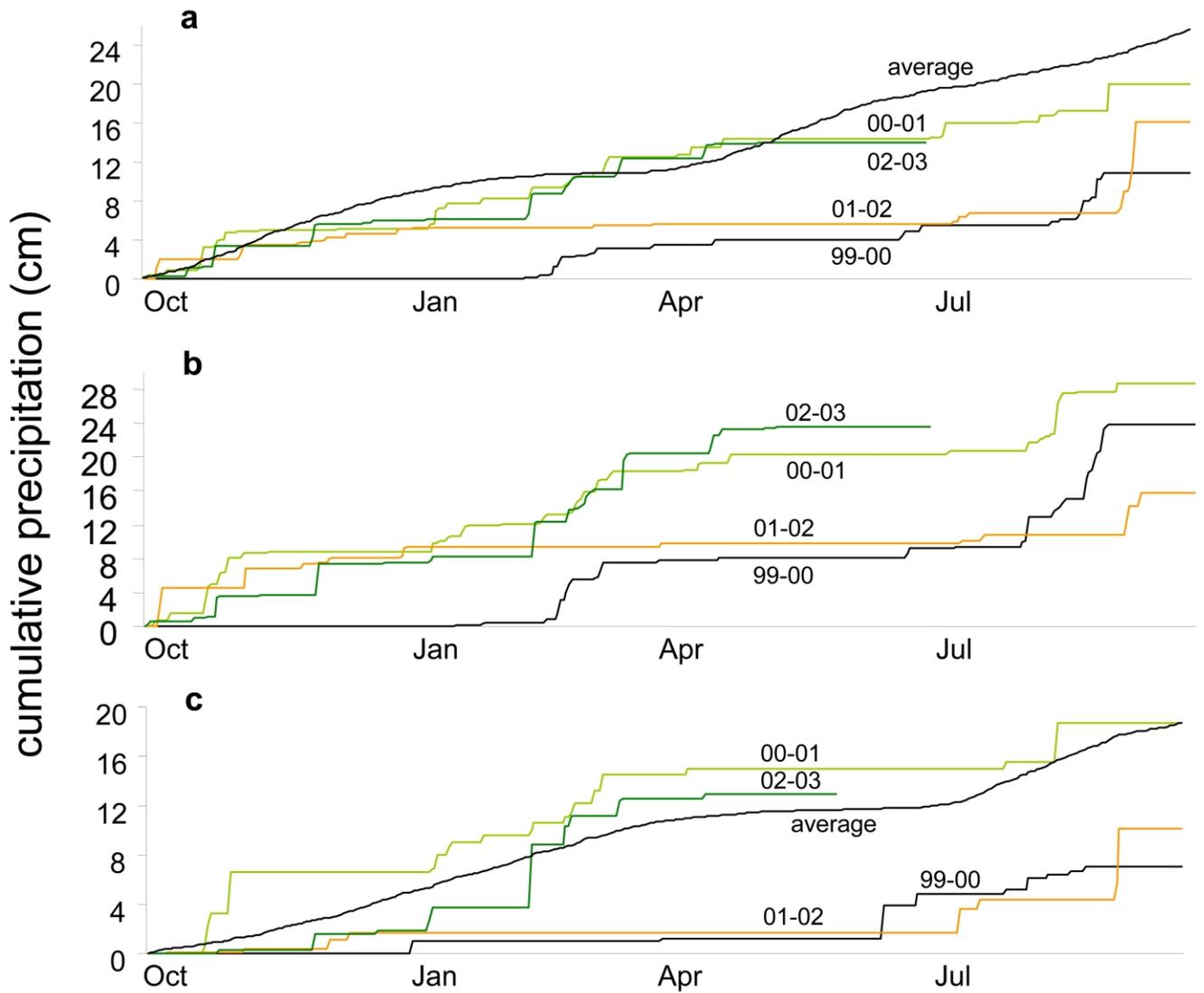
We computed the variance among one-time-step growth rates in the last 1,000 time steps of simulations of population growth with versus without seed banks, as described above, and computed the 95% confidence intervals for this variance term using the bias-corrected percentile method.

### **Temporal Autocorrelation in Precipitation**

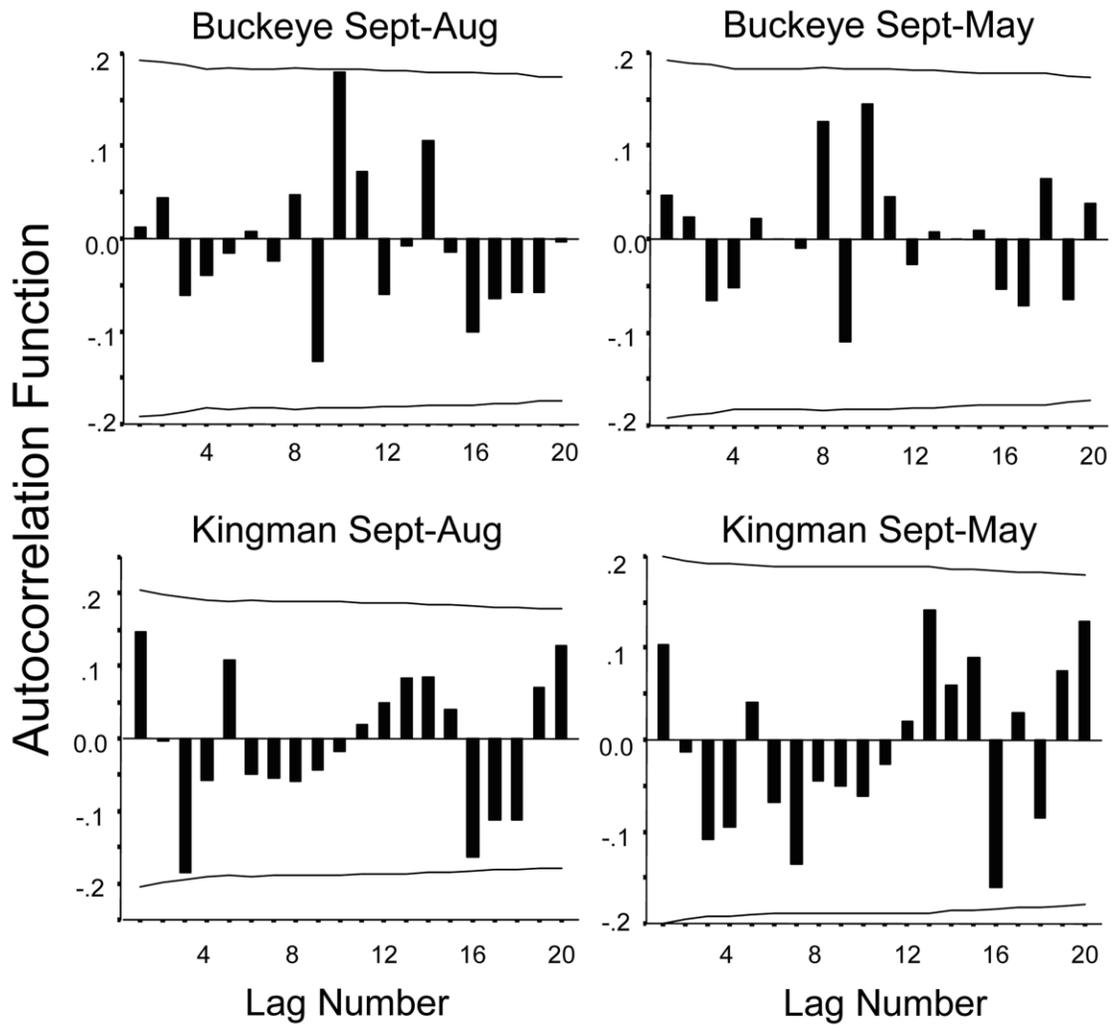
Variation in precipitation drives variation in demography in our study species (“Results”), as in many desert plants (Kadmon and Schmid 1990; Watson et al. 1997; Pierson and Turner 1998). Temporal autocorrelation in vital rates affects population dynamics and life-history evolution (Kalisz and McPeck 1993; Tuljapurkar and Istock 1993; Gabriel and Ferriere 2004; Pike et al. 2004; Ivarsson et al. 2005; Tuljapurkar and Haridas 2006), including what simulation methods can be used to estimate long-run stochastic growth rates (Tuljapurkar et al. 2003). To test for temporal autocorrelation in precipitation, we calculated the autocorrelation function for time series of precipitation from the Kingman weather station near the perennial study sites (1901–2003) and the Buckeye weather station near the annual study sites (1893–2003) using SPSS (ver. 11.0.1), up to lag  $k = 20$  years. We analyzed records of precipitation in two periods: 12 months from September to August (i.e., the full year, beginning with the first month when germination is likely) and 9 months from September to May (the core period of germination, seedling survival, and seed production). The autocorrelation function is the covariance of the time series with itself, given a lag of  $k$ , normalized by the variance of the time series. It varies from 1 to  $-1$ , ranging from perfect correlation to perfect anticorrelation, respectively.

The autocorrelation function should be applied only where the time series is stationary, that is, where there is no trend. We tested for trend by performing regressions of each time series against the year the data were collected. If precipitation declined or increased over the period of records, such a regression should be significant; none was significant ( $P > .24$ ).

If the value of the autocorrelation function is more extreme than two times the standard error for 0, one rejects the null hypothesis of 0 autocorrelation at that lag. Nearly significant autocorrelations occur at a lag of 10 years for precipitation per 12 months at the Buckeye weather station and at a lag of 3 years for precipitation per 12 months at the Kingman weather station, but no lags approach significance for total precipitation during the 9-month period (September to May) when germination, seedling survival, and seed production occur (fig. A2). We conclude that the variation in precipitation that affects vital rates in our study species may be viewed as independent and identically distributed, or white noise.



**Figure A1:** Cumulative precipitation in the 4 years of the study and on average at weather stations nearest the perennial (*a*, *b*) and annual (*c*) study sites, respectively. The data in *a* were recorded at the Kingman airport, and the data in *b* were recorded at a remote station maintained by the Bureau of Land Management (BLM). These two weather stations bracket the range of elevation of the perennial study populations: the station at the Kingman airport is about 12 km from the Private site and is 100 m lower in elevation, and the BLM station is 7.2 km from the BLM site and about 530 m higher in elevation. The data in *c* were collected at the Buckeye station, which is 8 and 20 km from the Buckeye and Hassayampa sites, respectively (elevation 300 m).



**Figure A2:** Autocorrelation function for time series of precipitation (lag  $k = 1-20$  years) at the Buckeye weather station near the annual study sites (1893–2003) and the Kingman weather station near the perennial study sites (1901–2003). Autocorrelation of total precipitation in two periods is calculated: September–August and September–May. The horizontal lines indicate two times the standard error for 0 autocorrelation.

**Table A1**

Estimated soil seed density ( $S_{(t)}$ ,  $S_{(t-1)}$ ), seed rain density ( $G_{(t-1)}$ ), seedling density ( $L_{(t)}$ ), and consequent survival of seeds in the soil (per 365 days) in two natural populations of the Sonoran Desert annual *Oenothera arizonica* and three natural populations of the Mojave Desert perennial *Oenothera californica* ssp. *avita*

Year, species, and population	$S_{(t-1)}$ (seeds/m <sup>2</sup> )	$S_{(t)}$ (seeds/m <sup>2</sup> )	$G_{(t-1)}$ (seeds/m <sup>2</sup> )	$L_{(t)}$ (seedlings/m <sup>2</sup> )	$s_p$ (days)	$s_s$ (days)	$s_w$ (days)	Seed survival (per 365 days)
2001–2002:								
Annual:								
Buckeye	20.96 (62)	27.99 (65)	1,092	.76	0	273	71	.0204
Hassayampa	69.03 (64)	28.88 (63)	573	.03	0	273	71	.0372
Perennial:								
Private	87.9 (68)	492.12 (66)	2,587	1.26	48	158	130	.1184
State	71.97 (65)	93.09 (67)	312	2.56	44	189	101	.1794
BLM	89.33 (64)	141.75 (66)	128	1.68	47	161	131	.6137
2002–2003:								
Annual:								
Buckeye	27.99 (65)	31.91 (57)	0	5.03	0	310	82	1.0000 <sup>a</sup>
Hassayampa	28.88 (63)	4.48 (58)	0	1.73	0	267	125	.2135
Perennial:								
Private	492.12 (66)	3.94 (66)	0	.21	52	263	56	.0089
State	93.09 (67)	3.00 <sup>b</sup> (67)	0	6.36	53	129	190	.0493
BLM	141.75 (66)	16.95 (46)	0	5.19	50	163	157	.1384

**Note:** The number of soil samples processed per site and year is shown in parentheses.

<sup>a</sup> Survival is estimated to be 1.0 because a greater density of seeds was found in the 2003 sample than in the 2002 sample, while seed production in 2002 was zero.

<sup>b</sup> No seeds were found in the 67 soil samples collected at the State site in 2003, hence the upper limit of soil seed density is 3.87 seeds/m<sup>2</sup>. We set soil seed density at a value (3.00) that is arbitrarily lower than this upper limit.

**Table A2**

Number of clones in natural populations of the Mojave and Great Basin Desert perennial *Oenothera californica* ssp. *avita*

	Private	State	BLM
2000–2001	11	102	67
2001–2002	0	75	222
2002–2003	0	42	138

**Table A3**

Bootstrapped confidence intervals (95%) of vital rates in two populations of the annual *Oenothera arizonica* and three populations of the perennial *Oenothera californica* ssp. *avita*

	Annual		Perennial		
	Buckeye	Hassayampa	Private	State	BLM
$g$ (wet)	.01, .61	.01, .56	.01, .61	.01, .56	.01, .59
$g$ (dry)	<.01, .21	<.01, .17	<.01, .21	<.01, .21	<.01, .23
yss	<.01, .57	<.01, .56	<.01, .57	<.01, .58	<.01, .57
$F_a$ (wet)	50.4, 63.4	745, 1,116	4, 4	21.8, 25.4	116.3, 143.0
$s_j$ (wet)			.06, .20	.44, .50	.42, .48
$s_a$ (wet)			<.01, .25	<.01, .25	<.01, .25
$s_a$ (dry)			<.01, .04	.01, .07	.04, .24
$C$			0	.15, 20.3	.14, 21.9
$F_c$ (wet)			0	6.12, 13.0	9.22, 21.23

**Note:**  $g$  = germination fraction; yss = soil seed survival per 365 days.  $F_a$  reported for the annual populations is the product of  $F_a$  and  $s_j$  (hence, seeds produced per germinated seed); what is reported for the perennial populations is  $F_a$  alone (seed production per adult or fruiting seedling), not its product with  $s_j$  (seedling survival). The rate of clone survival ( $s_c$ ) is assumed to be equal to adult survival ( $s_a$ ). There were no clones produced ( $C$ ) and therefore no seed production by clones ( $F_c$ ) at the Private site.

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**App. from M. E. K. Evans et al., “Bet Hedging via Seed Banking”**

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