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Bet Hedging via Seed Banking in Desert Evening Primroses (*Oenothera*, Onagraceae): Demographic Evidence from Natural Populations

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ABSTRACT: Bet hedging is one solution to the problem of an unpredictably variable environment: fitness in the average environment is sacrificed in favor of lower variation in fitness if this leads to higher long-run stochastic mean fitness. While bet hedging is an important concept in evolutionary ecology, empirical evidence that it occurs is scant. Here we evaluate whether bet hedging occurs via seed banking in natural populations of two species of desert evening primroses (*Oenothera*, Onagraceae), one annual and one perennial. Four years of data on plants and 3 years of data on seeds yielded two transitions for the entire life cycle. One year was exceptionally dry, leading to reproductive failure in the sample areas, and the other was above average in precipitation, leading to reproductive success in four of five populations. Stochastic simulations of population growth revealed patterns indicative of bet hedging via seed banking, particularly in the annual populations: variance in fitness and fitness in the average environment were lower with seed banking than without, whereas long-run stochastic mean fitness was higher with seed banking than without across a wide range of probabilities of the wet year.

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This represents a novel, unusually rigorous demonstration of bet hedging from field data.

All organisms live in a variable environment. Depending on the temporal and spatial scale of this variation (relative to the organism's life span, mobility, and potential rate of population growth), solutions may aim at maintaining homeostasis (via plasticity, heterophylly, dispersal, or other behavioral responses) or generating genetic diversity or polymorphism within or among individuals (hypermutation, chasmogamous vs. cleistogamous flowers, seed polymorphism, and other forms of bet hedging; Lloyd 1984; Meyers and Bull 2002). Bet hedging has fascinated evolutionary ecologists because it is one explanation for traits that otherwise might seem maladaptive (Stearns 1992; Roff 2002). Under bet hedging, mean fitness (i.e., the fitness of the organism were it to constantly experience the average environment) is sacrificed in favor of reduced variance in fitness if this leads to higher long-term fitness (Seger and Brockman 1987; Philippi and Seger 1989; Hopper 1999; Menu and Desouhant 2002; Evans and Dennehy 2005). Hence, bet hedging has been described as a trade-off between the mean and the variance of fitness. For example, in a seed-banking annual plant, a high intrinsic rate of increase, via immediate germination, is sacrificed in favor of the risk-spreading properties of variably delayed germination. A trait that seems maladaptive (delayed germination, risking mortality as a seed) makes evolutionary sense in light of a full account of fitness in an unpredictably variable environment.

While bet hedging is well understood theoretically (Cohen 1966; Ellner 1985) and the phenomenon is frequently cited, empirical evidence that it occurs in nature is still scarce (Hopper 1999; Clauss and Venable 2000; Menu and Desouhant 2002). With respect to seed or egg banking, one approach has been to correlate variation among pop-

ulations in germination or hatch fraction with variation in the risk associated with emergence into those environments; notable examples include those of Philippi (1993) and Clauss and Venable (2000). This approach follows from the theoretical prediction that the fraction of propagules emerging should increase with the probability of years of reproductive success (Cohen 1966). However, in some cases, the predicted pattern was observed because of maternal effects (Philippi 1993) or predictive adaptive plasticity (Clauss and Venable 2000); in other cases, the patterns have not been as expected (see discussion in Clauss and Venable 2000 and references therein). A few studies have analyzed the fitness consequences of different emergence patterns (Kalisz and McPeek 1993; Clauss 1999; Menu et al. 2000). But conspicuously lacking has been any analysis showing that a putative bet-hedging trait reduces fitness variation, increases long-run stochastic fitness, and decreases fitness in the average environment.

In this study, we ask whether bet hedging occurs via seed banking in natural populations of two closely related desert evening primroses, one of which is annual and the other perennial. It has been suggested that selection for seed dormancy should be weaker in iteroparous perennials because iteroparity, like variably delayed germination, spreads the risk of reproductive failure across years (Rees 1993, 1994; Thompson et al. 1998; Tuljapurkar and Wiener 2000; but see Ellner et al. 1998; Schippers et al. 2001). That is, iteroparity and seed banking may, to some degree, be partially substitutable forms of bet hedging. However, germination trials with these two species revealed similar levels of seed dormancy (Evans 2003). Hence, we evaluate whether bet hedging occurs via seed banking in both. We collected 4 years of data on plant demography and 3 years of data on seed demography. We construct population models and perform stochastic simulations of population growth in order to evaluate three patterns expected under bet hedging: that the long-run stochastic population growth rate should be higher, that the growth rate in the average environment should be lower, and that variance in yearly growth rates should be lower with seed banking than without (see table 1 in Philippi and Seger 1989).

Methods

Species and Sites

We used two closely related species of evening primrose (*Oenothera*, Onagraceae): the Mojave and Great Basin Desert perennial *Oenothera californica* ssp. *avita* (hereafter, the perennial) and the Sonoran Desert annual *Oenothera arizonica* (hereafter, the annual; Klein 1970; Wagner 1998; Evans et al. 2005). Both are winter recruiting: germination typically occurs in the autumn. Plants flower in the spring

and disperse seeds in the late spring or early summer (May–June). We studied multiple naturally occurring populations, three of the perennial (Private, State, and Bureau of Land Management [BLM]) and two of the annual (Buckeye and Hassayampa; see details in the appendix in the online edition of the *American Naturalist*), both because demography in desert plants is variable spatially as well as temporally (e.g., Kadmon and Schmida 1990) and because a robust comparison at the species level requires replication at the population level. We show precipitation data collected at weather stations nearest these perennial and annual study sites in the years of the study.

Plant Demography

We sampled survival and seed output per plant (annual and perennial populations) and clone production per plant (perennial populations) in four years (1999–2000 through 2002–2003). Plants were censused after the first significant autumn rain (>25 mm; stimulating germination) and approximately every 8 weeks thereafter, until flowering had ended the following spring. Individuals were relocated by their coordinates within marked quadrats or belt transects within study areas. Seed output was estimated by multiplying counts of fruits per plant (on every plant) and seeds per fruit (from population- and year-specific samples; appendix). While collecting data in the perennial populations, we distinguished three types of plants: seedlings, adults, and clonal rosettes (clones; for details, see appendix).

Seed Demography

Estimates of the density of ungerminated, viable seeds in the soil allowed us to calculate both germination fraction and seed bank survival. We collected soil samples after germination had ended but before new seeds were dispersed, in the spring of the years 2001–2003; seeds were then sorted out of the soil. We calculated germination fraction by dividing seedling density (the total density of seedlings that emerged over the germination season) by the sum of seedling density and viable, ungerminated seed density (estimated in soil samples). Seed survival in the soil was calculated by solving dynamical equations for the density of ungerminated, viable seeds in one year in terms of the seed density the previous year, seed rain, and seed germination (see appendix).

Population Models

Given a postreproductive census, the annual populations can be modeled with a scalar equation that tracks only the number of seeds (appendix). The life cycle graph corre-

sponding to this model is shown in figure 1*a*. In this model, g is the fraction of seeds that germinate, s_j is the fraction of seedlings that survive to produce at least one fruit, F_a is the mean number of seeds produced by plants that make at least one fruit, and s_s, s_w, and s_p are the rates of seed survival in three intervals per year (from the time of seed rain to the time of germination decision, from the time of germination decision to the time of soil seed bank sampling, and from the time of soil seed bank sampling to the time of seed rain, respectively). The model for the perennial populations is a transition matrix model, also reflecting a postreproductive census, with three life stages (seeds, adults, and clones; appendix). The corresponding life cycle graph is shown in figure 1*b*. In addition to the parameters in the annual model, the perennial model includes adult survival (s_a), 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 per surviving adult or clone (C).

Testing Predictions of Bet Hedging

A bet-hedging trait should increase long-run stochastic fitness and reduce mean fitness (the growth rate if the population were to constantly experience the average environment). This pattern is typically described using terms that are appropriate for life histories that can be modeled with a scalar equation (i.e., unstructured populations), like the annual populations studied here: arithmetic mean growth rate is sacrificed in favor of higher geometric mean growth rate (Seger and Brockman 1987; Philippi and Seger 1989; Hopper 1999; Menu and Desouhant 2002). In the case of structured life histories, like the perennial populations studied here, the appropriate analogue of the arithmetic mean growth rate is the dominant eigenvalue of the weighted mean transition matrix, and the appropriate analogue of the geometric mean growth rate is the dominant Lyapunov exponent of the stochastic process that generates the transition matrices (Tuljapurkar 1989; Ferriere and Gatto 1995). Here we use the more inclusive terms "average environment growth rate" (λ_a) and "long-
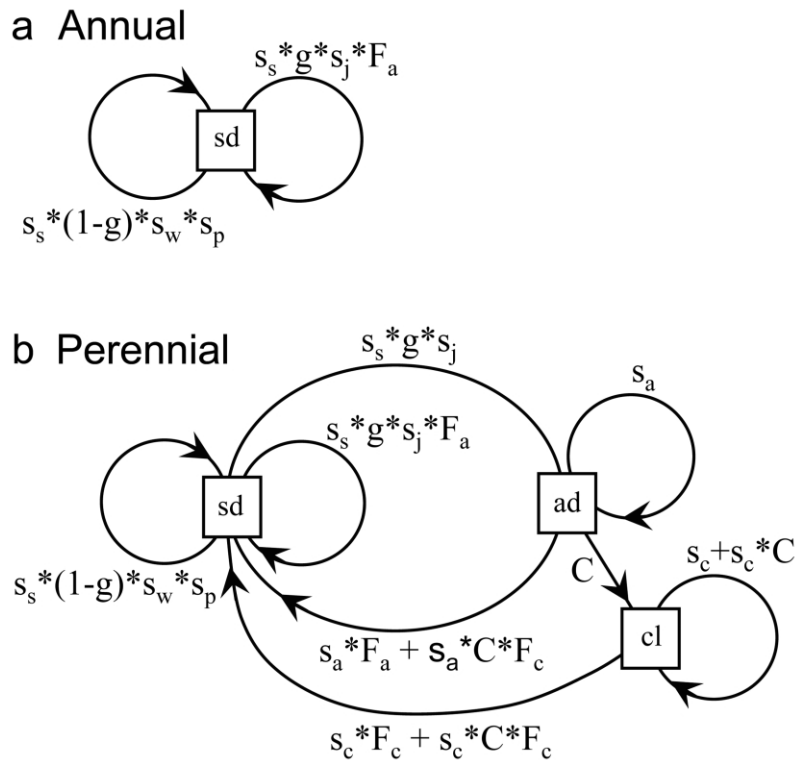

Figure 1: Life cycle diagrams of the models used for (*a*) populations of the Sonoran Desert winter annual *Oenothera arizonica* and (*b*) the Mojave and southern Great Basin Desert perennial *Oenothera californica* ssp. *avita*. Three classes of individuals are possible: seeds (*sd*), adults (*ad*), and clones (*cl*). Definitions of these classes and the parameters are in the text and in the appendix in the online edition of the *American Naturalist*.

run stochastic growth rate" (λ_s) rather than arithmetic and geometric mean growth rate, respectively, because this study includes both scalar and matrix models.

We estimated long-run stochastic growth rates numerically via simulations of population growth in ULM (Unified Life Models, ver. 4.0; see details in appendix). The fact that the dry year led to total reproductive failure in the sample areas (see "Results") suggests that seed banking can buffer the most extreme form of variation in reproductive success possible: it can prevent extinction (in the annual populations). To investigate a more interesting scenario, we modified the reproductive success of the dry year to a small nonzero value (consistently across all sites and analyses) chosen to reflect the fact that the observed zero reproduction was obtained in a subset of the population and hence is subject to sampling variation (see appendix). By doing so, we make our test of bet hedging more conservative in the sense that we reduce the putative benefit of the seed banking strategy. The years for which we have data for the entire life cycle (2001–2003) yield two transitions: one year was dry (2001–2002) and one wet (2002–2003). Using long-term weather records as a guide to choose a single probability of the wet versus the dry year for analysis is problematic (the resulting long-run stochastic growth rate is too high; see appendix, "Testing Predictions of Bet Hedging"), so we calculated λ_s across the entire range of the probability of the wet year (p; 0–1.0). This approach has the advantage of revealing just how robust the patterns expected under bet hedging are to the distribution of environmental states. We found no significant temporal autocorrelation in 100-year records of precipitation from weather stations adjacent to the study sites (appendix), so we treated environmental variation as independent and identically distributed in the simulations. Based on an evaluation of convergence dynamics (see appendix), we ran each simulation for 6,000 time steps: 5,000 to reach convergence and the last 1,000 to sample λ_s. We then recalculated λ_s after removing the seed bank (germination fraction is set to 1, and the simulation is rerun). Average environment growth rates were calculated analytically (annual populations) or numerically (perennial populations; appendix) across the entire range of p. In addition to its effects on long-run stochastic and average environment growth rates, a bet-hedging trait should reduce fitness variation. We compared 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 (see appendix).

Confidence limits for the long-run stochastic and average environment growth rates and variance among single-year growth rates, with and without seed banking, were computed with a bootstrap procedure. The bootstrapping was executed so that each replicate set of vital rates, leading to a distinct estimate of the growth rate (annual populations) or transition matrix (perennial populations), had a sister that was identical, except that the germination fraction was set to 1 (seed banking was eliminated; see appendix). The bootstrapping was conducted at a baseline value of the probability of the wet year (p^*). In three populations (those with $\lambda < 1$ in the dry year and $\lambda > 1$ in the wet year), p^* is the value of p that leads to a long-run stochastic growth rate of 1.00. Elsewhere we used $p = 0.1$ (either to suppress or to boost the long-run stochastic growth rate; see appendix). We modeled a wide range of possible values for the most variable and potentially uncertain parameters, including seed parameters (germination fraction and soil seed survival), for which we did not have information from marked individuals tracked over time, and adult and clone survival and clone production, in which case the inability to observe what happened belowground obscured survival and growth.

Results

Demography and Weather

Two study seasons were relatively dry (1999–2000 and 2001–2002), and two were relatively wet (2000–2001 and 2002–2003; fig. A1 in the online edition of the *American Naturalist*). In all five study populations, seedling survival and seed output were low in the two dry years and higher in the two wet years (table 1). Adult survival (nonclonal survival after at least one reproductive bout) in the perennial populations was generally low: in most cases, 5% or less (table 1; survival of clonal rosettes is assumed to be the same as adult survival). Germination fraction and seed bank survival varied considerably: 3% or fewer of seeds germinated in the dry year 2001–2002 compared with 5%–68% in the two wet years (2000–2001 and 2002–2003; table 1). Yearly seed bank survival ranged from 0.9% to 100% without consistent differences according to species or year type (table A1 in the online edition of the *American Naturalist*).

All of our analyses focus on the last two study seasons, which included an exceptionally dry year compared with long-term records of weather variation (2001–2002) and a year of above-average precipitation (2002–2003; fig. 2). The dry year 2001–2002 was a year of reproductive failure. Seedlings failed to produce seeds in the study areas at all five sites, and at the three perennial sites, plants already in reproductive classes failed to produce seeds (table 1). At one perennial site (Private), production of clonal rosettes failed as well. Consequently, in three populations (the two annual populations plus the Private site of the perennial), the predicted asymptotic growth rates (deterministic single-year λ's) were equivalent to the yearly rate

Table 1: Estimated vital rates in two natural populations of the Sonoran Desert annual *Oenothera arizonica* and three natural populations of the Mojave Desert perennial *Oenothera californica* ssp. *avita* over the study period (1999–2003)

	Annual populations			Perennial populations			
Vital rate and year	Buckeye	Hassayampa	Mean	Private	State	BLM	Mean
Seedling survival (s_j):							
1999–2000	.06 (340)	.02 (402)	**.04**	...	...	...	...
2000–2001	.48 (410)	.40 (420)	**.44**	.28 (425)	.29 (300)	.07 (538)	**.19**
2001–2002	.00 (84)	.00 (7)	**.00**	.00 (255)	.00 (228)	.00 (213)	**.00**
2002–2003	.50 (896)	.75 (283)	**.56**	.12 (43)	.47 (610)	.45 (654)	**.45**
Seed output by adults (F_a):							
1999–2000	31 (17)	9 (7)	**25**	...	...	...	...
2000–2001	346 (198)	254 (167)	**304**	876 (120)	183 (108)	149 (42)	**486**
2001–2002	NA	NA	NA	0 (2)	0 (4)	0 (6)	**0**
2002–2003	112 (452)	1,174 (212)	**451**	4 (6)	24 (287)	138 (294)	**81**
Germination fraction (g):							
2000–2001	.237	.076		.080	.045	.099	
2001–2002	.026	.001		.003	.027	.012	
2002–2003	.136	.279		.051	.679	.234	
Summer seed survival (s_s):							
2001	.054	.085		.397	.411	.806	
2002	1.0	.323		.033	.345	.414	
Winter seed survival (s_w):							
2001–2002	.469	.527		.468	.622	.839	
2002–2003	1.0	.589		.484	.209	.428	
Spring seed survival (s_p):							
2001				.755	.813	.939	
2002				.510	.646	.763	
2003				.504	.657	.759	
Adult survival (s_a):							
2000–2001				.004 (249)	.053 (399)	.100 (40)	**.038**
2001–2002				.017 (121)	.037 (108)	.133 (45)	**.044**
2002–2003				.500 (2)	.00 (4)	.00 (6)	**.083**
Seed output by clones (F_c):[a]							
2000–2001				0 (11)	8.9 (102)	1.4 (67)	**5.9**
2001–2002				NA	0 (75)	0 (222)	**0**
2002–2003				NA	9.6 (42)	14.6 (138)	**13.4**
Clone production (C):							
2001–2002				NA	9.2	14.3	
2002–2003				NA	5.5	6.3	

Note: Survival of clonal rosettes is assumed to be the same as survival of adults ($s_c = s_a$). In parentheses is the number of plants censused. Means of vital rates that were estimated from individual-level data are shown in bold for each species and year, weighted by the number of plants. NA = not applicable.

[a] Seed output by clones is less than seed production by adults because so many clones did not fruit, whereas most adults were first-year adults, which by definition produced at least one fruit.

of seed bank survival and were well below the replacement value of 1.0 (table 2). In the remaining two perennial populations (State and BLM sites), clonality buffered reproductive failure more than seed banking, and λ was equal to the clone-to-clone transition probability. At the State site, λ was less than 1.0, but at the BLM site, the number of clonal rosettes more than doubled from 2001 to 2002; hence, λ > 2.0. In the wet year (2002–2003), four out of the five study populations had predicted asymptotic growth rates that would lead to increased population size; the predicted asymptotic growth rate of the perennial pop-

ulation at the Private site would lead to population decline (table 2).

Growth Rates With versus Without Seed Banks

We compared average environment and long-run stochastic growth rates with and without seed banks across the entire range of *p*, the probability of the wet year (fig. 3). In four populations, average environment growth rates were higher after removing the seed bank, as expected under bet hedging, regardless of the probability of the wet
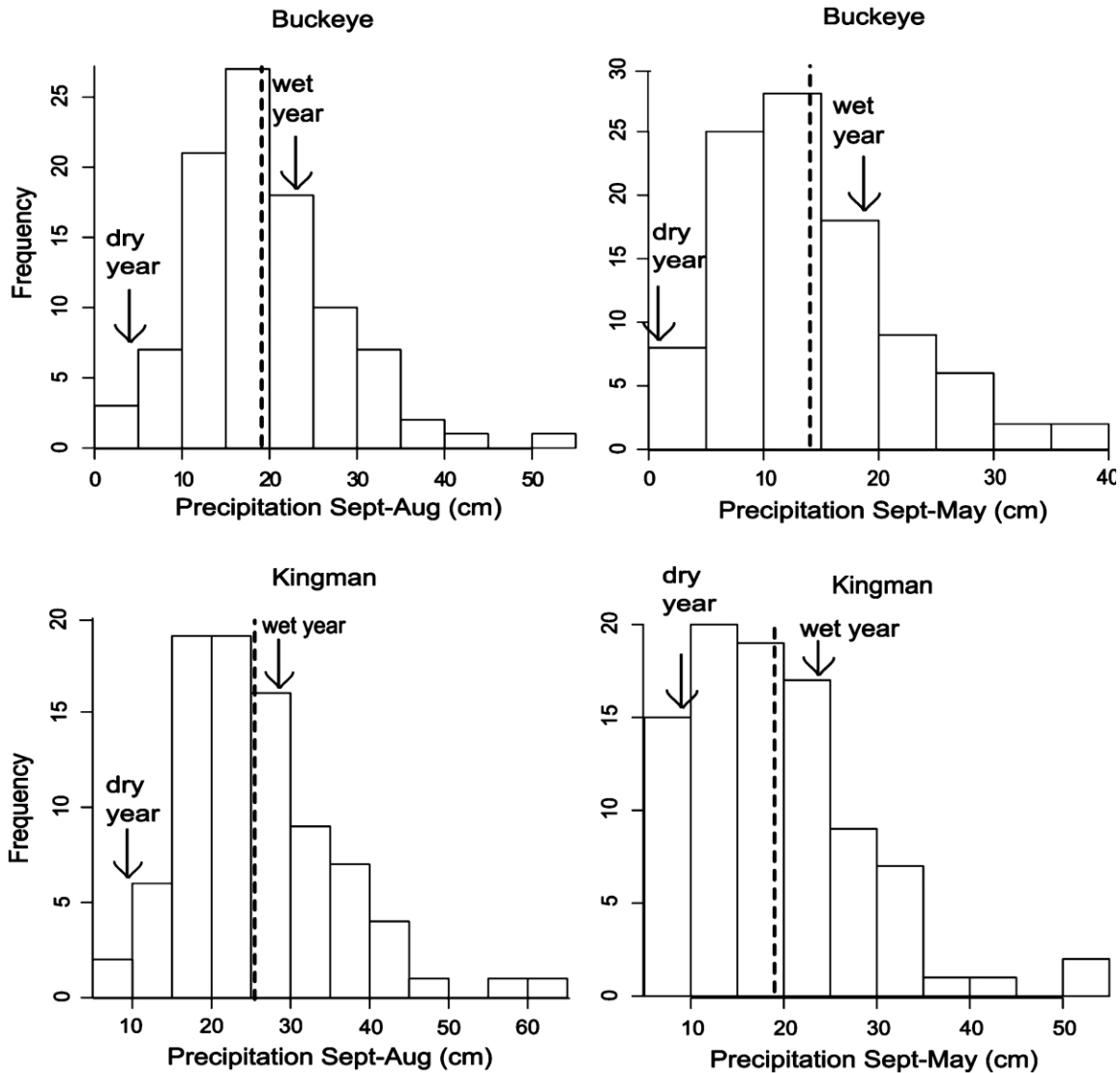
Figure 2: Frequency histograms of precipitation from historical records at Buckeye, Arizona (1893–2003), near the annual study sites, and Kingman, Arizona (1901–2003), near the perennial study sites. The panels show total precipitation in the 12 months between September and August and in the 9-month period during which germination, seedling survival, and seed production occur (September–May). Vertical dashed lines indicate the mean of each distribution, and arrows mark precipitation in the last 2 years of the study, the dry year (2001–2002) and the wet year (2002–2003).

year (fig. 3). Long-run stochastic growth rates were higher with the seed bank than without, as expected under bet hedging, across a wide range of p in four populations: the two annual populations and the perennial populations at the Private and State sites (fig. 3). There is no value of p at which these two patterns were observed simultaneously in the perennial populations where $\lambda < 1$ or $\lambda > 1$ in both years (Private, BLM), but there are wide ranges of values of p over which both were obtained in the two annual populations (Buckeye, $p = 0.01–0.47$; Hassayampa, $p =$

$0.01–0.58$; fig. 3) and in one perennial population (State, $p = 0.01–0.67$; fig. 3).

The confidence intervals for long-run stochastic and average environment growth rates are large (table 2) because our bootstrapping procedure included a wide range of possible values for certain vital rates (table A3 in the online edition of the *American Naturalist*). For this reason, we compare the growth rates with and without seed banks of each bootstrap replicate, where the resampled vital rates (other than germination fraction) are constant in each

Table 2: Population growth rates (λ) using field estimates of vital rates from two populations of the annual *Oenothera arizonica* and three populations of the perennial *Oenothera californica* ssp. *avita*

	λ_{dry}[a]	λ_{wet}	λ_s	λ_a	Var(λ)	p^*
Annual:						
Buckeye:						
With SB	.03 (.00, .56)	8.48 (.04, 10.31)	1.00 (.03, 2.55)	5.267 (.06, 6.42)	7.91 (.00, 31.16)	.620
Without SB	.00 (.00, .05)	56 (.53, 44.21)	1.71 (.08, 2.31)	34.72 (.33, 21.57)	21.11 (.04, 323.6)	.620
Hassayampa:						
With SB	.04 (.00, .58)	79.49 (.58, 213.2)	1.00 (.03, 3.78)	31.11 (.32, 83.56)	13.61 (0.08, 12,266)	.391
Without SB	.01 (.00, .05)	284.4 (9.54, 641.5)	.55 (.05, 1.48)	111.2 (3.74, 250.8)	27.86 (47.30, 94,141)	.391
Perennial:						
Private:						
With SB	.10 (.01, .56)	.08 (.01, .57)	.07 (.01, .48)	.04 (.02, .51)	.54 (.00, .05)	.100
Without SB	.03 (.01, .06)	.10 (.01, .50)	.03 (.01, .06)	.02 (.02, .08)	.07 (.00, .06)	.100
State:						
With SB	.38 (.05, 1.05)	2.94 (.08, 6.92)	1.00 (.12, 2.05)	1.84 (.14, 4.29)	1.94 (.00, 10.83)	.588
Without SB	.38 (.03, 1.06)	4.17 (.54, 26.85)	.96 (.26, 3.21)	2.47 (.40, 16.18)	3.89 (.03, 163.3)	.588
BLM:						
With SB	2.04 (.13, 3.83)	6.26 (.16, 26.75)	1.80 (.16, 3.42)	1.90 (.21, 4.31)	.53 (.00, 57.55)	.100
Without SB	2.04 (.13, 3.85)	25.85 (1.59, 113.1)	1.83 (.18, 3.76)	2.66 (.41, 11.36)	1.07 (.08, 998.5)	.100

Note: Deterministic single-year growth rates are shown for a dry year (2001–2002) and a wet year (2002–2003). Long-run stochastic (λ_s) and average environment (λ_a) growth rates and the variance among single-year growth rates (Var(λ)) are reported using the probability of the wet year (p^*). Growth rates and variance among growth rates are shown with (g = field estimate) and without seed banking (SB; g = 1.0), followed by 95% confidence intervals.

[a] Seedling survival and seed output of 0 in the dry year (2001–2002) were changed to 0.003 and 25 seeds, respectively, before calculating any growth rates. Hence, the growth rates in the annual populations in the dry year are not necessarily 0 when seed banking is eliminated.

comparison. The patterns reported above for average environment growth rates are very robust across bootstrap replicates (table 3). Of the two populations that show the expected bet-hedging pattern in long-run stochastic growth rates at the probability of the wet year (p^*) at which the bootstrapping was conducted, the pattern is quite robust to the range of reasonable values of vital rates in one case (Hassayampa) but decidedly not robust in the other (State; table 3).

Variance in Growth Rates With versus Without Seed Banks

Variance in growth rates was reduced in the presence of seed banks compared with that in the absence of seed banks, regardless of the probability of the wet year, in four of five populations (fig. 3). At the probability of the wet year that leads to a long-run stochastic growth rate of 1.0 (p^*; Buckeye, Hassayampa, State), the variance among growth rates is twice to three times greater if seed banking is eliminated (table 2). The confidence intervals for variance of one-time-step growth rates are broad, with large areas of overlap between simulations with and without seed banks, though the maximal values are much greater without seed banks (table 2). The variance among growth rates is greater without seed banks in a large fraction of the 1,000 bootstrap replicates, indicating that the pattern

expected under bet hedging is robust to alternative values for vital rates (table 3).

Discussion

Empirical confirmation of bet hedging is rare (Hopper 1999; Menu and Desouhant 2002). Bet hedging has been described as a trade-off between the mean and the variance of fitness (Philippi and Seger 1989); that is, reduced variance in fitness (a benefit) comes at a cost in terms of fitness in the average environment (arithmetic mean fitness) such that long-run stochastic (i.e., geometric) mean fitness is increased. These three patterns expected under bet hedging have never been demonstrated to occur simultaneously, based on data from a natural population.

The first two bet-hedging patterns were observed regardless of the probability of the wet versus the dry years in four out of five populations (at all but the Private site and all but the BLM site, respectively; fig. 3). That is, the variance among single-year growth rates was lower in stochastic simulations of population growth with seed banks than without, and average environment growth rates increased with the elimination of seed banking. These two patterns were quite robust to alternative values of vital rates generated by bootstrapping. The third pattern was observed over a broad range of probabilities of the wet versus the dry year in four populations (two annual and
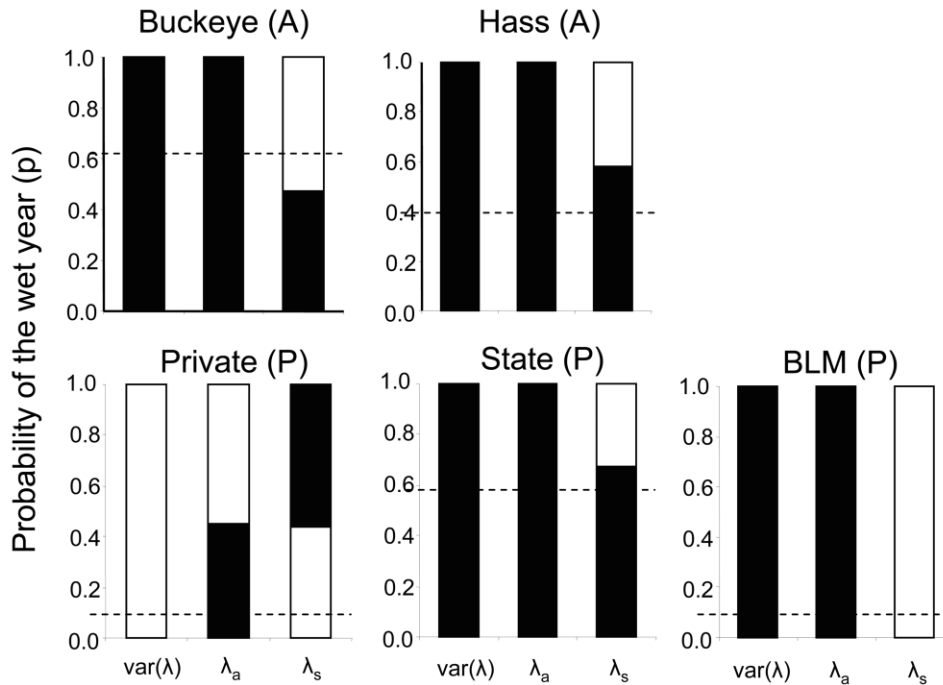
Figure 3: Effect of *p*, the probability of the wet year, on three patterns expected under bet hedging. They are (1) that the variation among growth rates is greater without seed banking than with, (2) that the average environment growth rate is greater without seed banking than with, and (3) that the long-run stochastic growth rate is greater with seed banking than without. A bar is filled where the condition is true at the value of *p*. The horizontal dashed line indicates the value of *p* yielding the results reported in table 2. The effect of *p* is shown using data from two populations of the annual *Oenothera arizonica* and three populations of the perennial *Oenothera californica* ssp. *avita* (*A* = annual, *P* = perennial).

two perennial populations; fig. 3): stochastic mean growth rates were greater in simulations of population growth with seed banks than without. This was true at the probability that leads to a long-run stochastic growth rate of 1.0 in one annual population (Hassayampa) and one perennial population (State; table 2). All three patterns were obtained simultaneously in three populations across a wide range of *p*: the two annual populations (Buckeye, *p* = 0.01–0.47; Hassayampa, *p* = 0.01–0.58) and one perennial population (State, *p* = 0.01–0.67).

It is not surprising that we obtained the three patterns expected under bet hedging, given that the 2 years that we collected data for the entire life cycle happened to be an exceptionally dry year in which no seeds were produced in the sample areas followed by a year of above-average precipitation and deterministic asymptotic growth rates greater than 1.0. This is exactly the scenario that Cohen (1966) explored in his pioneering models of bet hedging via seed banking: an annual plant population experiences a variable environment leading to either reproductive success or reproductive failure. One of the most obvious conclusions of Cohen's (1966) model (and that of Ellner [1985]) is that the most successful germination strategy

must be a germination fraction less than 1 whenever there is any probability of reproductive failure. Any population (or genotype) expressing a germination fraction of 1 would immediately become extinct on encountering a year of reproductive failure. Here we obtain the population dynamical patterns expected under bet hedging under the conservative assumption that the actual seed production takes on nonzero values whenever the estimated seed production was null. Only when the probability of the good year becomes too high does the long-run stochastic growth rate fail to be higher with seed banking than without (as in Kalisz and McPeek 1993).

Several lines of evidence suggest that the bet-hedging effect of seed banking is strong in the two annual populations compared with that seen in only one of three perennial populations (State). The average environment growth rates of the two annual populations are 6.6 and 3.6 times greater without a seed bank than with (Buckeye and Hassayampa, respectively) compared with just 1.3 times greater at the State site, and the long-run stochastic growth rate declines without a seed bank by a factor of 0.55 in the annual population at the Hassayampa site compared with just 0.96 in the perennial population at the

Table 3: Number of comparisons between bootstrapped growth rates and variance in growth rates with and without seed banking (SB; out of 1,000 each) that are in the direction expected under bet hedging

	Annual		Perennial		
	Buckeye	Hassayampa	Private	State	BLM
λ_s with SB > λ_s without SB	271	867	884	54	92
λ_a with SB < λ_a without SB	995	1,000	145	998	996
Var(λ) with SB < Var(λ) without SB	992	1,000	537	968	974

Note: λ_s, λ_a = bootstrapped growth rates; Var(λ) = variance in growth rates. Based on data from two natural populations of the annual *Oenothera arizonica* and three natural populations of the perennial *Oenothera californica* ssp. *avita*.

State site (table 2). Further, the bootstrapping exercise indicated that, at the State site, the latter pattern was not robust to alternative values for vital rates. The three bet-hedging patterns were not obtained in the remaining two perennial populations, where the asymptotic growth rates suggest decline in both years (Private) or increase in both years (BLM). This result is consistent with the idea that selection for bet hedging via seed banking should be weaker in iteroparous perennials than in annuals (Rees 1993, 1994; Thompson et al. 1998; Tuljapurkar and Wiener 2000). However, the fact that we observed either $\lambda < 1$ or $\lambda > 1$ in both years at two sites (Private, BLM) implies that these 2 years may not be representative overall and makes it impossible to obtain the bet-hedging patterns there. The data from the remaining study site (State) suggest that bet hedging may occur via seed banking in perennial populations, at least under some combinations of vital rates. Our study of bet hedging via seed banking in perennial populations cannot be considered conclusive.

The confidence limits for growth rates and variance in growth rates with versus without seed banks overlap broadly because we modeled a wide range of possible values for certain vital rates (table A3). For example, soil seed survival per year varied from 0.0 to 0.6 among bootstrap replicates (table A3). The long-run stochastic mean growth rates are sensitive to some of these widely varying vital rates, particularly soil seed survival (annual populations) and adult or clone survival (perennial populations) in years of reproductive failure (Evans 2003). As a result, differences between growth rates with and without seed banks are obscured by the variation among bootstrap replicates caused by new values for vital rates. Hence, we compared the growth rates of paired bootstrap replicates, where all vital rates are the same except germination fraction. In spite of this wide variation in vital rates, most of the bet-hedging patterns are quite robust to alternative values for vital rates (table 3). The exception is the long-run stochastic growth rate at the State site (a perennial population), where the bet-hedging effect appears to be marginal, as discussed above.

While the results from our analysis of the fitness con-

sequences of seed banking are consistent with bet hedging, the data are also indicative of adaptive plasticity in germination behavior. Germination fractions were low in the dry year and higher in the two wet years that they were estimated (table 1) rather than fixed on an optimal strategy for all years (in opposition to the prediction by Cohen [1966]). This plasticity is adaptive in the sense that it is positively correlated with the reproductive success of seeds that do germinate (as in Pake and Venable 1996; Clauss and Venable 2000). Predictive adaptive plasticity is not bet hedging, but we should not be surprised to find evidence of both within populations, given that environments typically are partially but not completely predictable (Cohen 1967; Evans and Dennehy 2005). Ellner (1985) found that the predictions for evolutionarily stable strategies of germination in a variable environment were qualitatively similar between models with constant and variable germination.

The combination of analyses presented here is unique. Some of the patterns expected under bet hedging that we focus on here have been analyzed separately in three other studies (Kalisz and McPeek 1993; Clauss 1999; Menu et al. 2000). With data very similar to ours (2 years: one good, one bad), Kalisz and McPeek (1993) showed that the long-run stochastic growth rate of an annual plant is greater with its natural seed bank than without. Menu et al. (2000) showed that the long-run stochastic growth rate of a population with a mixed strategy of emergence timing (adult beetles emerging after 1 or 2 years of diapause) is greater than those of populations with either pure strategy (emerging after 1 year or after 2 years). Clauss (1999) showed that germination fractions less than 1 reduce both arithmetic mean (average environment) fitness and variance in fitness across years in a desert annual plant. In three populations in this study, we show all three effects.

Few other studies have analyzed the fitness consequences of variation in putative bet-hedging traits. Venable et al. (1995) computed the relative fitness of seeds differing in within-season germination timing in an annual plant without seed banks, revealing the conditions under which risky versus conservative germination strategies performed

well. Simons and Johnston (2003) predicted when bolting is favored over delaying reproduction on the basis of field data for a monocarpic plant, and the departure from this rule set was taken as evidence of conservative bet hedging in the face of unpredictable growing season length. Additional analyses of the fitness consequences of putative bet-hedging traits, either from individuals that can be identified and vary in those traits or from manipulating the trait in data-based models, will strengthen our understanding of the ecology and evolution of bet hedging in the wild, including the consequences of bet-hedging traits for persistence and species coexistence. For example, it would be worthwhile to understand the degree to which bet-hedging traits might buffer increased weather variation associated with global climate change (Boyce et al. 2006) and extinction in fragmented landscapes (Stocklin and Fischer 1999; Piessens et al. 2004) or mediate the coexistence of native and nonnative species in invaded communities (Levine and Rees 2004).

Acknowledgments

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