

REPORTS

Ecology, 88(5), 2007, pp. 1086–1090
© 2007 by the Ecological Society of America

BET HEDGING IN A GUILD OF DESERT ANNUALS

D. LAWRENCE VENABLE¹

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 95721 USA

Abstract. Evolutionary bet hedging encapsulates the counterintuitive idea that organisms evolve traits that reduce short-term reproductive success in favor of longer-term risk reduction. It has been widely investigated theoretically, and many putative examples have been cited including practical ones such as the dormancy involved in microbe and weed persistence. However, long-term data on demographic variation from the actual evolutionarily relevant environments have been unavailable to test for its mechanistic relationship to alleged bet hedging traits. I report an association between delayed germination (a bet hedging trait) and risk using a 22-year data set on demographic variation for 10 species of desert annual plants. Species with greater variation in reproductive success (per capita survival from germination to reproduction \times per capita fecundity of survivors) were found to have lower average germination fractions. This provides a definitive test using realistic data on demographic variance that confirms the life history prediction for bet hedging. I also showed that the species with greater long-term demographic variation tended to be the ones with greater sensitivity of reproductive success to variation among years in growing-season precipitation.

Key words: *bet hedging; delayed germination; desert annuals; long-term demographic variation; seed bank.*

INTRODUCTION

Bet hedging is pervasive in human endeavors as is reflected in terms such as “hedge funds” or expressions like, “a bird in the hand is worth two in the bush” or “don’t put all your eggs in one basket” (Seger and Brockmann 1987). Bet hedging is presumed to be pervasive in the biological world as well and may be involved in any characteristic of an organism that buffers it from temporal environmental variation. Putative examples include invertebrate silk-ballooning dispersal (Bell et al. 2005), the perennial life cycle (Tuljapurkar 1990), variable diapause in animals from crustaceans (Hairston and Munns 1984) and mosquitoes (Andreadis 1990) to sponges (Fell 1995) and fish (Martin 1999), resistance of weeds to eradication (Roberts and Feast 1972, Swanton and Weise 1991), variable offspring size in frogs (Crump 1981), and disease dynamics (Henderson et al. 1999, Stumpf et al. 2002). The concept is usually defined in terms of a trade-off between mean and variance of some performance criterion such as population growth, return on investment, or Darwinian fitness (Seger and Brockmann 1987). Organisms with a bet hedging trait should then have higher long-term

success, measured as geometric mean success or some other index of long-term growth rate in a variable environment.

The classic theoretical example of bet hedging is delayed germination in desert annuals, which was first modeled by D. Cohen (Cohen 1966). Delayed germination buffers variation in reproductive success much as cash under the pillow or a conservative financial investment buffers a risky investment. The best a non-germinating seed can do is survive while a germinating seed may either die without leaving any descendants or make 100s or even 1000s of new seeds. Thus producing a fraction of dormant seeds is the hedge against the variation associated with germination. When this variation is larger, the germination fraction favored by natural selection is lower (Ellner 1985). Bet hedging has been widely investigated theoretically (e.g., MacArthur 1972, Gillespie 1974, Venable and Lawlor 1980, Bulmer 1984, Sasaki and Ellner 1995, Mathias and Kiski 2002, Valleriani 2005).

While many models and putative examples of bet hedging exist, no empirical evidence has been available that directly assesses temporal variation in survival and reproduction in the evolutionarily relevant natural environment and its association with putative bet hedging traits. Conclusive demonstration of bet hedging requires such a demonstration of its association with greater environmental variation (risk). I provide such

Manuscript received 6 September 2006; revised 15 November 2006; accepted 18 December 2006. Corresponding Editor: B. E. Kendall.

¹ E-mail: venable@email.arizona.edu

evidence here for delayed germination of desert annual plants. I have collected long-term demographic data on a guild of co-occurring desert annuals and determined the relationship between risk and bet hedging.

MATERIALS AND METHODS

My laboratory has measured germination, survival, fecundity and dormant seed bank levels for desert winter annuals at the Desert Laboratory in Tucson, Arizona, USA. The data comes from a long-term project on the population and community dynamics of desert annuals that was initiated in 1982 at the University of Arizona Desert Laboratory (Venable and Pake 1999). This site has been fenced and ungrazed since 1907. Meteorological information is collected daily at the Desert Laboratory. Since 1982, 72 permanent plots for censusing desert winter annuals have been established along a 250-m transect through a gently sloped creosote bush flat. These plots have been visited regularly each year following each autumn and winter rain event to document winter annual seed germination, which usually occurs between October and early January. Each year since 1982 individual plants have been mapped at germination and followed until death in March or April to determine survival and lifetime reproduction. Seed dynamics have been monitored intensively since 1989 by sampling viable non-germinating seeds with 180 23-cm² soil cores per year (Venable and Pake 1999). The seed samples are collected during February, which is after the germination season but before new seeds fall in the March/April reproductive season. By combining the density of seeds germinating determined from the mapping plots (N) with the density of seeds not germinating determined from the seed samples (S), I have calculated the fraction of seeds germinating ($G = N/(N + S)$) for 14 years for these unmanipulated natural populations. Per capita reproductive success associated with germination in the different years was calculated from data on per capita survival from germination to reproduction and per capita fecundity of survivors. Specifically, "per capita reproductive success" was defined as the per capita probability of survival from germination to reproduction multiplied by the average per capita reproduction of survivors (i.e., the average number of seeds produced per germinating seed). The risk associated with germination was then measured as the geometric standard deviation of per capita reproductive success. The geometric standard deviation is the standard deviation of a logged variate transformed back to the original scale, $\exp(\text{SD}[\ln(\text{per capita reproductive success})])$. It has a parallel in the geometric mean (the mean of a logged variate transformed back to the original scale). It gives the standard deviation of proportional changes and is hence directly comparable among species with different fecundities. The log-transformation is also made appropriate by the multiplicative nature of population dynamics and because per capita reproduc-

tive success tends to have a log-normal distribution. Variation was calculated using 22 years of population dynamic data for the 10 species used in this study: *Pectocarya recurvata* (Boraginaceae), *Erodium cicutarium*, *Erodium texanum* (Geraniaceae), *Eriophyllum lanosum*, *Evax multicaulis*, *Monoptilon bellioides*, *Stylocline micropoides* (Asteraceae), *Plantago insularis* (= *P. fasciculata* var. *insularis*), *Plantago patagonica* (Plantaginaceae), and *Schismus barbatus* (Poaceae). These species were chosen because they are abundant enough in the long-term plots to calculate variation in per capita reproductive success and germination fraction.

The association of bet hedging with risk was assessed by calculating the Pearson product-moment correlation of average germination fraction with the geometric standard deviation of per capita reproductive success. While this is a very straightforward test, I also explored some more subtle sources of potential variation in the results. The uncertainty associated with using these particular 10 species was assessed by bootstrapping species to verify the robustness of the correlation. Also, each average germination fraction and geometric standard deviation is based on a finite sample of years (14 and 22, respectively). I evaluated the associated uncertainty by resampling the years used for these calculations with bootstrapping and then recalculating their correlation many times. Finally, each annual estimate of germination fraction and reproductive success was based on a finite number of plants and hence measured with uncertainty. While this should not bias the calculation of average germination fraction, the geometric SD measurement will be slightly biased by the inclusion of a small fraction of the within-year variance. I used bootstrap resampling to estimate the within-year standard error for each species in two of the 22 years and determined that the correction for the among-year variance was very small (on the order of 1%). Because the variance component correction was so small, I discontinued these calculations and conducted the other analyses without this correction. All resampling calculations used 10 000 iterations.

The sensitivity of reproductive success to growing-season precipitation was explored with regression. While major cohorts of seedlings have germinated from October through early January over the years, the most frequent germination times have been late November and December. As most growth occurs in response to January through March precipitation, we used the sum of precipitation for these months in the regressions. Reproductive success and precipitation were log-transformed prior to analysis to remove right skewing, which otherwise gives strong influence to a few extreme values.

RESULTS

The average germination fraction is lower in species that experience greater variation in per capita reproductive success if they germinate, as was predicted by bet hedging theory ($r = -0.78$, $P < 0.05$; Fig. 1). When the

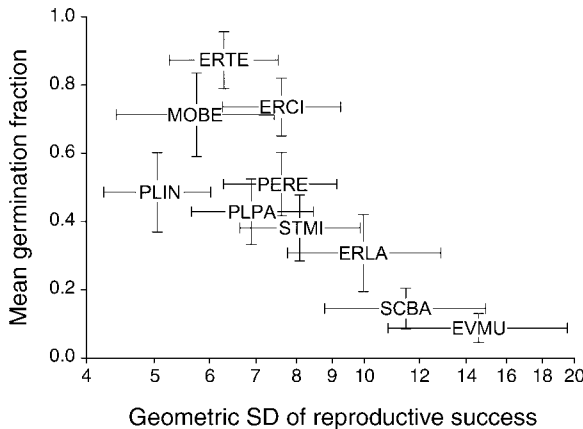


FIG. 1. Mean germination fraction of 10 species of desert annuals plotted against variation in per capita reproductive success (average number of seeds produced per germinating seed). Germination is averaged over 14 years. Demographic variation over 22 years is given as the geometric standard deviation, $\exp(\text{SD}[\ln(\text{per capita reproductive success})])$. Pearson's $r = -0.78$; $P < 0.005$ (calculated from the point estimates). When species are bootstrapped, 99% of 10 000 resampled correlations are negative. When years are bootstrapped, 100% of 10 000 resampled correlations are negative. Bootstrap details are in *Materials and methods* and *Results*. The markers for the data points are the abbreviations given by the first two letters of the genus and species names (see *Materials and methods*). The error bars are plus or minus one bootstrapped standard deviation.

uncertainty associated with using these particular 10 species to test the bet hedging prediction was assessed by bootstrapping species, 99% of the resampled correlations were still negative. When years were resampled to assess the uncertainty connected with using a finite sample of years, all 10 000 correlations were still negative. Thus the correlation appears to be robust to the particular species and years studied.

These species, while coexisting in the same physical location are experiencing different levels of demographic variation upon germination, presumably due to differences in physiology and life history. Much of the year-to-year variation in per capita reproductive success in each species is explained by variation in growing-season precipitation (January–March; Fig. 2). Greater sensitivity to precipitation leads to higher variance: species with steeper slopes of reproductive success vs. precipitation in Fig. 2 tend to have higher among-year demographic variation in Fig. 1 ($r = 0.89$; this is partly due to the standard deviation of y and the slope of y on x being correlated by definition). Differences in the variability of per capita reproductive success (due in part to differences in sensitivity to precipitation) constitute the different levels of risk which selects for different levels of bet hedging (Fig. 3).

DISCUSSION

Previous evidence of bet hedging has come in several forms. Phenotypes with presumed fitness costs inter-

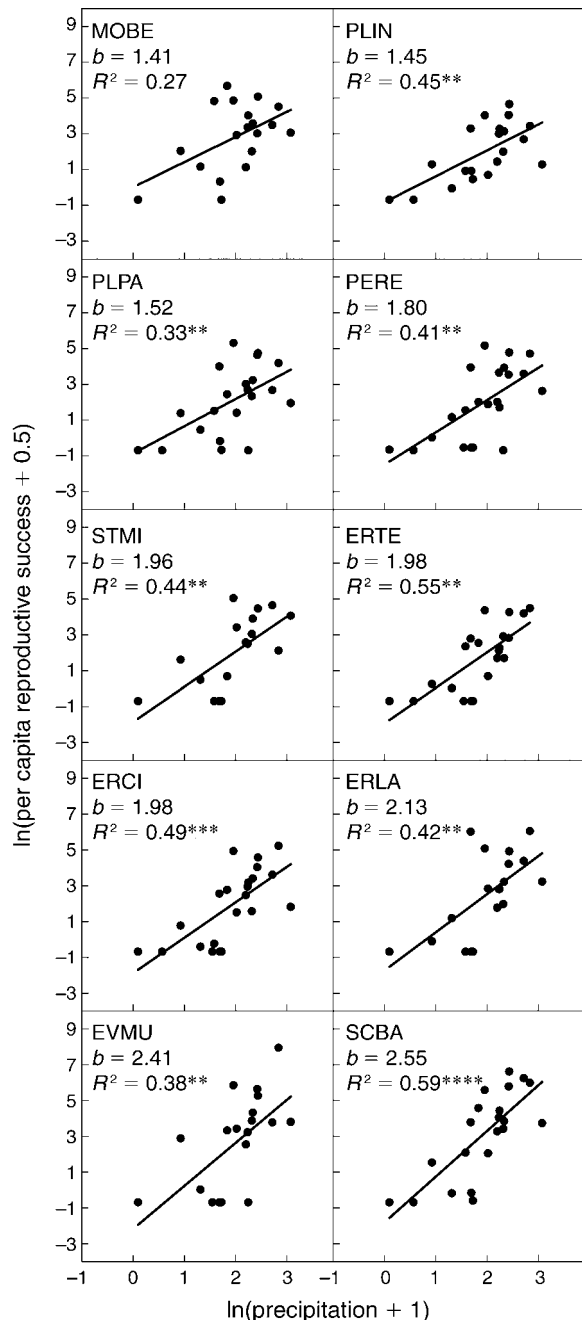


FIG. 2. Graphs of per capita reproductive success of each species plotted against growing-season precipitation. Per capita reproductive success is the average number of seeds produced per germinating seed. Growing-season precipitation is the sum of daily precipitation for January through March. Panels are ordered from shallowest to steepest slopes (b). The species abbreviations are the first two letters of the genus and species names. Significance is reported as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

pretable as bet hedging adaptations are widely taken as prima facie evidence of bet hedging (such as low or fractional germination or hatching, e.g., Glennon et al. 2006, Matsuo 2006). There are many such observations

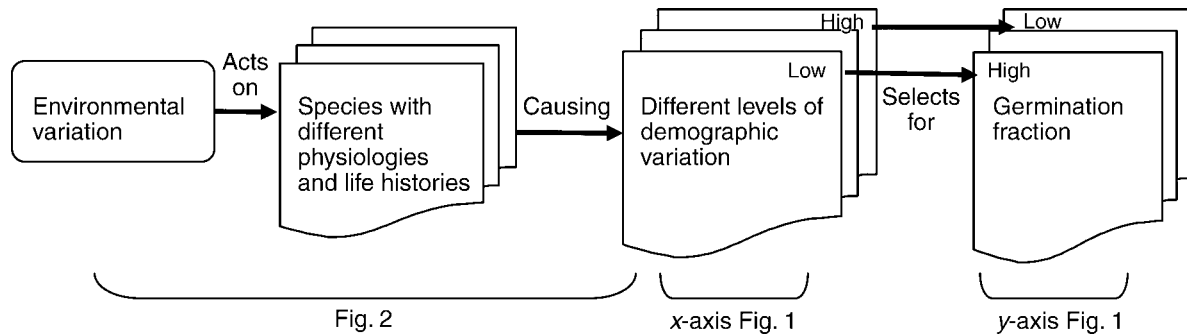


FIG. 3. Schematic showing how environmental variation selects for bet hedging (low germination fraction).

in the literature. However, they are mostly speculative and have been criticized as providing weak support for the idea of bet hedging (Hopper 1999, Evans and Dennehy 2005). Some studies determine a specific putative risk factor that could select for bet hedging (e.g., some mosquitoes have extended variable egg diapause and have larvae that depend on unpredictable water in tree holes, summarized in Evans and Dennehy 2005). One such study showed that the fractional hatching rate of a diapausing anostracan shrimp in ephemeral vernal pools matched quantitative predictions based on mortality rates estimated from larval development time and pool durations (Philippi et al. 2001). Better yet are studies that link the degree of expression of the putative bet hedging trait (e.g., degree of dormancy) with the magnitude of a surrogate for risk across a range of risk levels (e.g., low mean annual precipitation; Philippi 1993, Claus and Venable 2000). However, it is often uncertain exactly how variation in such a putative risk factor translates through the vagaries of organismal and population biology into variation in per capita reproductive success. Thus it is unclear how far to interpret equivocal or negative patterns (Hopper 1999). Several studies have parameterized stochastic simulations, inferring long-term population behavior from one or a few years of field data on survival and fecundity. These studies have shown that simulations with field-measured diapause dynamics often have higher long-term success (e.g., geometric mean) than simulations without diapause (Kalisz and McPeck 1993, Menu et al. 2000, Evans et al. 2007) or reduced arithmetic mean and variance with diapause (Claus 1999, Evans et al. 2007).

The present paper measures variation in per capita reproductive success directly using long-term demographic data to test for the association of greater bet hedging with greater risk. Species that experience greater demographic variation associated with germination were shown to have lower average germination fractions. All of the long-term data comes from unmanipulated populations of desert annuals growing in undisturbed natural habitat. This is likely to be the evolutionarily relevant germination and variance environment for these

species. Thus this data on a guild of desert annuals provides a definitive test of bet hedging by quantifying the purported selective mechanism in nature. Such a test has not been previously available because of the difficulty of collecting long-term data on demographic variance in natural habitats.

The species that experience greater variance in per capita reproductive success were shown to be more responsive to growing-season precipitation. This was presumed to be due to differences in physiology and life history. My collaborators and I are exploring the basis of this elsewhere and it appears that the demographic variation and variation in sensitivity to precipitation are due, at least in part, to a trade-off among species between growth rate and water use efficiency (Angert et al. 2007; T. E. Huxman et al., *unpublished manuscript*).

These data also reveal an interesting community pattern: a guild of co-occurring plants with a spectrum of demographic variances and correlated germination. Such life history differences have been implicated in structuring plant communities and accounting for stable species coexistence in variable environments (Chesson and Huntly 1988, Chesson 2000). So the life history pattern of demographic variance and germination fraction shown here not only validates a long-standing life history prediction about bet hedging, but it also provides an intriguing window on how physiologies and life histories are deployed in community structure.

ACKNOWLEDGMENTS

Funding was provided by NSF grants BSR 9107324, DEB 9419905 (LTREB), DEB 0212782 (LTREB), and DEB 0453781. Thanks to the following for stimulating ideas and data collection for this paper: Sandy Adondakis, Amy Angert, Greg Barron-Gafford, Amy Bell, Tony Caprio, Maria Claus, Ben Collins, Jonathan Cox, Michelle Davis, Norm Douglas, Jonathan Duke, Carrie Enquist, Gordon Fox, Kathy Gerst, Kevan Gilliam, Christine Golightly, Alice Halloran, Amelia Hazard, Jonathan Horst, Tani Hubbard, Travis Huxman, Renee Janaway, Amanda Jaksha, Greg Ketner, Oxana Kougot, Holly Lawson, Kristen McCoy, Chris McDonald, Ken Moriuchi, Cathie Pake, Marissa Pantastico, Catherine Pearson, Jim Pearson, Stephanie Roberts, Pilar Sanchez, Marcelo Schneider, Sabrina Stebens, Michelle Stubbs, Michael Wagenheim, and Brian Weeks.

LITERATURE CITED

- Andreadis, T. G. 1990. Observations on installment egg hatching in the brown salt-marsh mosquito, *Aedes cantator*. *Journal of the American Mosquito Control Association* 6: 727–729.
- Angert, A. L., T. E. Huxman, G. A. Barron-Gafford, K. L. Gerst, and D. L. Venable. 2007. Linking growth strategies to long-term population dynamics in desert annuals. *Journal of Ecology* 95:321–331.
- Bell, J. R., D. A. Bohan, E. M. Shaw, and G. S. Weyman. 2005. Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research* 95: 69–114.
- Bulmer, M. G. 1984. Delayed germination of seeds: Cohen's model revisited. *Theoretical Population Biology* 26:367–377.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Chesson, P. L., and N. Huntly. 1988. Community consequences of life-history traits in a variable environment. *Annales Zoologici Fennici* 25:5–16.
- Clauss, M. J. 1999. Life history strategies in variable environments. University of Arizona, Tucson, Arizona, USA.
- Clauss, M. J., and D. L. Venable. 2000. Seed germination in desert annuals: an empirical test of adaptive bet hedging. *American Naturalist* 155:168–186.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* 12: 119–129.
- Crump, M. L. 1981. Variation in propagule size as a function of environmental uncertainty for tree frogs. *American Naturalist* 117:724–737.
- Ellner, S. 1985. ESS germination strategies in randomly varying environments. 1. Logistic-type models. *Theoretical Population Biology* 28:50–79.
- Evans, M. E. K., and J. J. Dennehy. 2005. Germ banking: bet-hedging and variable release from egg and seed dormancy. *Quarterly Review of Biology* 80:431–451.
- Evans, M. E. K., R. Ferriere, M. J. Kane, and D. L. Venable. 2007. Bet hedging via seed banking in desert evening primroses (*Oenothera*, Onagraceae): demographic evidence from natural populations. *American Naturalist* 169:184–194.
- Fell, P. E. 1995. Deep diapause and the influence of low temperature on the hatching of the gemmules of *Spongilla lacustris* (L) and *Eunapius fragilis* (Leidy). *Invertebrate Biology* 114:3–8.
- Gillespie, J. H. 1974. Natural-selection for within-generation variance in offspring number. *Genetics* 76:601–606.
- Glennon, V., L. A. Chisholm, and I. D. Whittington. 2006. Three unrelated species, 3 sites, same host monogenean parasites of the southern fiddler ray, *Trygonorrhina fasciata*, in South Australia: egg hatching strategies and larval behaviour. *Parasitology* 133:55–66.
- Hairston, N. G., and W. R. Munns. 1984. The timing of copepod diapause as an evolutionarily stable strategy. *American Naturalist* 123:733–751.
- Henderson, I. R., P. Owen, and J. P. Nataro. 1999. Molecular switches—the ON and OFF of bacterial phase variation. *Molecular Microbiology* 33:919–932.
- Hopper, K. R. 1999. Risk-spreading and bet-hedging in insect population biology. *Annual Review of Entomology* 44:535–560.
- Kalisz, S., and M. A. McPeck. 1993. Extinction dynamics, population growth and seed banks: an example using an age-structured annual. *Oecologia* 95:314–320.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper and Row, New York, New York, USA.
- Martin, K. L. M. 1999. Ready and waiting: delayed hatching and extended incubation of anamniotic vertebrate terrestrial eggs. *American Zoologist* 39:279–288.
- Mathias, A., and E. Kisdí. 2002. Adaptive diversification of germination strategies. *Proceedings of the Royal Society B* 269:151–155.
- Matsuo, Y. 2006. Cost of prolonged diapause and its relationship to body size in a seed predator. *Functional Ecology* 20:300–306.
- Menu, F., J. P. Roebuck, and M. Viala. 2000. Bet-hedging and variability in life cycle duration: bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* 132:724–734.
- Philippi, T. 1993. Bet-hedging germination of desert annuals: variation among populations and maternal effects in *Lepidium lasiocarpum*. *American Naturalist* 142:488–507.
- Philippi, T., M. Simovich, E. Bauder, and J. Moorad. 2001. Habitat ephemerality and hatching fractions of a diapausing Anostracan (Crustacea: Branchiopoda). *Israel Journal of Zoology* 47:387–395.
- Roberts, H. A., and P. M. Feast. 1972. Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research* 12:316–324.
- Sasaki, A., and S. Ellner. 1995. The evolutionarily stable phenotype distribution in a random environment. *Evolution* 49:337–350.
- Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? Pages 182–211 in P. H. Harvey and L. Partridge, editors. *Oxford surveys in evolutionary biology*. Oxford University Press, Oxford, UK.
- Stumpf, M. P. H., Z. Laidlaw, and V. A. A. Jansen. 2002. Herpes viruses hedge their bets. *Proceedings of the National Academy of Sciences (USA)* 99:15234–15237.
- Swanton, C. J., and S. F. Weise. 1991. Integrated weed management: the rationale and approach. *Weed Technology* 5:657–663.
- Tuljapurkar, S. 1990. Delayed reproduction and fitness in variable environments. *Proceedings of the National Academy of Sciences (USA)* 87:1139–1143.
- Valleriani, A. 2005. Algebraic determination of the evolutionary stable germination fraction. *Theoretical Population Biology* 68:197–203.
- Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in space and time. *Oecologia* 46:272–282.
- Venable, D. L., and C. E. Pake. 1999. Population ecology of Sonoran Desert annual plants. Pages 115–142 in R. H. Robichaux, editor. *The ecology of Sonoran Desert plants and plant communities*. University of Arizona Press, Tucson, Arizona, USA.