Evolutionary
Bet Hedging

Hedging One's Evolutionary Bets, Revisited

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Evolutionary bet-hedging involves a trade-off between the mean and variance of fitness, such that phenotypes with reduced mean fitness may be at a selective advantage under certain conditions. The theory of bet-hedging was first formulated in the 1970s, and recent empirical studies suggest that the process may operate in a wide range of plant and animal species.

Some of the more interesting recent extensions of evolutionary theory concern exceptions to the rule that natural selection favours traits that maximize an individual's expected number of surviving offspring. For example, an individual's eventual inclusive fitness can sometimes be increased by tactics that entail the production of fewer than the maximum possible number of offspring, when the phenotypes in question concern sex allocation or interactions among kin. Reduced mean fitness can also evolve if the environment varies temporally, in which case phenotypes with low variances of fitness may be favoured over alternatives with higher variances and higher mean fitnesses.

This trade-off between the mean and variance of fitness has been called 'bet-hedging' ever since Slatkin[1] wrote a commentary entitled 'Hedging one's evolutionary bets', concerning a model by Gillespie[2] showing how selection could reduce the variance of offspring numbers. Real environments always vary temporally, so it seems likely that many kinds of phenotype have attributes that serve at least in part to hedge bets. Here we briefly review the basic ideas and describe some recent empirical developments.

When the fitness of a genotype varies over generations, the appropriate measure of its relative growth rate is its *geometric mean* fitness, rather than its arithmetic mean fitness. The geometric mean of n numbers is the nth root of their product. If the numbers vary, then the geometric mean is always less than the arithmetic mean; in general, the geometric mean becomes smaller as the numbers being averaged become more variable. Thus the geometric mean fitness of a genotype can be increased by reducing the variance of its fitness (over generations), even if the reduction of variance also entails a reduction of the arithmetic mean. The principle is similar to risk aversion in utility theory; the cost of a negative deviation from the mean is larger than the benefit of an equivalent positive deviation.

Bet-hedging phenotypes may be *conservative* or *diversified*[3]. The spirit of conservative bet-hedging is captured in the adage, 'a bird in the hand is worth two in the bush'. A conservative phenotype avoids extremes. For example, suppose that years are 'good' or 'bad' with equal probability, and that the wild type produces, on average, 9 offspring in good years and 1 offspring in bad years, for an average of 5. Now introduce a mutant that produces 5 offspring in good years and 3 offspring in bad years, for an average of only 4. Despite its lower mean fitness, the mutant quickly goes to fixation because its geometric mean fitness (3.87) is much higher than that of the wild type (3.0). The mutant's best performance is much worse than the wild type's best, but its worst is better, and this is the key to its success.

The spirit of diversified bet-hedging is captured by another old saw, 'don't put all your eggs in one basket'. From a formal point of view the result is identical to that achieved by conservative bet-hedging: the geometric mean fitness (over generations) is increased by reducing the variance of the mean within-generation fitness experienced by a bet-hedging genotype. But the tactic used to achieve this reduced variance of fitness (for the genotype as whole, over generations) may involve *increasing* the phenotypic and fitness variances among individuals *within* generations.

For example, consider the situation set out in Table I. Strategy B

Table I. Fitnesses of two specialist and two bet-hedging phenotypes in a variable environment			

	Phenotype			
Year type	A	B	C	D
Good	1.0	0.6	0.785	0.8
Bad	0.58	1.0	0.785	0.79
Arithmetic mean	0.79	0.8	0.785	0.795
Geometric mean	0.762	0.775	0.785	0.795

Good and bad years occur randomly, with equal frequency. Phenotypes A and B are good- and bad-year specialists respectively, C is a conservative bet-hedger, and D is a diversified bet-hedger that expresses equal proportions of the A and B phenotypes. Within each kind of year, fitnesses are scaled to those of the better specialist. In an annual species the diversified tactic D would be evolutionarily stable against A, B and C, because it has the highest geometric mean fitness. In a perennial species the geometric mean *lifetime* fitnesses would approach the arithmetic means; given a sufficiently long mean lifetime, the specialist phenotype B could be stable against A, C and D.

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(the bad-year specialist) has both a higher expected fitness and a higher geometric mean fitness than strategy A (the good-year specialist), and will therefore be favoured by selection. Strategy C (a conservative bet-hedger) will be favoured over both A and B, even though it does not do best in either kind of year. But consider strategy D. Each year it randomly produces the phenotype of either A or B (in this example with equal probability). Its expected fitness in a good year or a bad year is the arithmetic mean of the fitnesses achieved by the two specialist phenotypes in that year. By averaging the fitnesses of the specialists, it achieves an even higher geometric mean fitness than C.

The phenotypic diversification produced by this form of bet-hedging is subtly different from that of a mixed ESS. In general, a mixed ESS may be produced either by a genetic polymorphism or by individual genotypes that express both phenotypes. A diversified bet-hedging strategy must be realized as the variable phenotypic expression of a single genotype[3,4]. The reason is that not all members of the equilibrium phenotype distribution necessarily have the same arithmetic or geometric mean fitness; indeed, some are often worse than any of the others, as judged by almost any standard. In the present example, strategy-D individuals that happen to express the A (good-year specialist) phenotype have lower expected and geometric mean fitnesses than those that express the B phenotype.

Recent interest in bet-hedging has focused on the germination behaviour of seeds, the diapause behaviour of insects, and parental control of offspring size.

Germination

The first treatment of diversified bet-hedging was Cohen's model for the germination of desert annuals[5]. In the simplest case there are two year types (say, good and bad) with Y_g and Y_b seeds produced by each germinating seed. Let p be the probability of a good year, and let s be the survivorship probability of a seed that remains dormant. Then the fitness of a given germination fraction G is

$$W(G) = GY + (1 - G)s \qquad (1)$$

with Y being replaced by Y_g or Y_b depending on the kind of year. The geometric mean fitness will then be

$$W(G) = |GY_g + (1 - G)s|^p |GY_b + (1 - G)s|^{(1-p)} \qquad (2)$$

An example is shown in Fig. 1. If bad years are so bad that no seeds mature ($Y_b = 0$), then the optimal germination fraction is

$$G = (pY_g - s)/(Y_g - s) \qquad (3)$$

which is close to p for all plausibly large values of Y_g. Seeds that germinate risk suffering a bad year, but seeds that do not germinate risk mortality while dormant. Thus a seed that remains dormant necessarily has a smaller expected contribution to future generations than does a seed that germinates, but there may be many years in which germination will prove universally lethal.

Cohen's model makes several testable predictions. First, seeds that do not germinate under good conditions in the first year should germinate under those same conditions in subsequent years. Second, within a species, the fraction of seeds from different sites that germinate in the first year (and in each subsequent year) should correlate with the average amount and predictability of rainfall at the sites. Third, each parent genotype should produce seeds that germinate in different years.

Preliminary results from a study by one of us (TP) support all three predictions. Seeds of the winter annual *Lepidium lasiocarpum* from Portal, Arizona were germinated in an environmental chamber set up to match the day and night soil temperatures and the photoperiod (throughout the year) at Portal. Each year, seeds were watered beginning in December and continuing until no more seeds germinated in that year. Sixty-four per cent of the seeds germinated in the first year, and 44% of the remaining seeds germinated in the second year. Seeds of *L. lasiocarpum* were also collected from three sites with different average amounts of rainfall. The fraction of seeds germinating in the first year was perfectly rank-correlated with mean rainfall. Seeds collected from individual plants germinated in both the first and second years.

Cohen's model has been extended in several directions. For example, if at the time of germination there exists a perceptible cue to the quality of the year, then each value of the cue becomes a case of the completely unpredictable model, with appropriately adjusted probabilities of the different year types[6]. Dormancy, dispersal and seed size are complementary and partially substitutable life-history responses to spatial and temporal environmental uncertainty[7]. If it is possible to disperse to patches that experience good and bad conditions independently of the current patch, then spatial escape may partly replace the temporal escape of dormancy[8]. Plants with larger seeds that can do relatively well in mediocre years should exhibit lower levels of bet-hedging dormancy than plants with smaller seeds, because they have a lower variance of expected reproductive success[7,9]. To the extent that a species is also affected by bet-hedging trade-offs involving time of flowering or other life-history events (see below), the choices made with respect to one event may affect the pay-off structure associated with each of the others[9,10].

Density-dependent competition for seedling survival and adult seed production also affect the pay-offs associated with a given germination response, and the fitnesses therefore become frequency dependent; ESS rather than optimization methods are required. Different mathematical forms for the density dependence (reciprocal yield[11], logistic growth[12], constant population size[13]) predict different ESS germination strategies. It is not clear, in general, whether genetic polymorphisms can be maintained under such conditions.

Diapause

Insects enter diapause to avoid unfavourable conditions, so diapause is analogous in some ways to seed dormancy. For species with several generations per year, there will come a time in the season when individuals should enter dia-

pause rather than developing directly. If unfavourable conditions always arrive on the same date, a population should abruptly switch from direct development to diapause[14-17]. But where the date of onset is unpredictable, a diversified strategy may be favoured in which a fraction of the individuals undergo direct development while the others enter diapause. There is evidence for this pattern in pitcher-plant mosquitoes (*Wyeomyia smithii*)[18], milkweed bugs (*Oncopeltus fasciatus*)[19], lace bugs (*Corythucha* spp.)[20], and other insects[21]. The probability of entering diapause should increase monotonically through the season, and the first few individuals to enter diapause should do so as soon as there is a significant probability that conditions will deteriorate badly; for many species this could occur very early in an otherwise long season. In a population of the mud-dauber wasp *Trypoxylon politum*, the proportion of individuals entering diapause increased from 0.1 to 0.88 over 12 weeks, with all individuals entering diapause thereafter[3].

In several species of insects, small proportions of larvae are known to diapause for two or more winters[3,21]. Scattered observations of this behaviour come mainly from laboratory rearing experiments, but they seem likely to reflect natural behaviour if entire seasons may occasionally be unsuitable for reproduction. Given current levels of interest in life-history evolution in general, and bet-hedging in particular, this syndrome has received surprisingly little attention.

Offspring size

If different egg sizes are favoured under different conditions, and if conditions vary among generations in an unpredictable way, then within-individual variation in egg size could be a diversified bet-hedging strategy. Cooper and Kaplan[22,23] derive this argument from a decision-theoretic point of view, but their 'intra-genomic strategy mixing' and 'adaptive coin flipping' operate on the familiar variance-reduction principle common to all bet-hedging models. They note that the intra-genomic strategy could be produced by

either within- or among-clutch variation in egg size. Variation among clutches could be distributed either within females (whose successive clutches would differ in egg size) or among females. In practice, variation within clutches is hard to distinguish from nonadaptive environmental noise[24]; variation among clutches may be easier, at least in principle, to distinguish from noise.

The clutch-size model of Smith and Fretwell[25] predicts a constant optimal offspring size; females with different amounts of resource should make different numbers of offspring, not different sizes of offspring. But in *Gambusia affinis*[26], *Ambystoma talpoideum*[27], *Bufo bufo*[28], the parasitic mistletoe *Phoradendron juniperinum* (T. Dawson, pers. commun.), and other organisms, larger or older females produce larger offspring. These correlations have been interpreted as possible instances of bet-hedging. Although they cannot be explained by the original Smith–Fretwell model, it is not obvious that they can plausibly be explained as bet-hedging, either.

As long as successive environments are imperfectly correlated, merely having more than one chance to reproduce will decrease the variance of lifetime reproductive success[29]. But given iteroparity, does a strategy that expresses different phenotypes (e.g. egg sizes) in a fixed sequence gain additional benefits of bet-hedging? Consider the simple case with two uncorrelated environments and two oppositely specialized phenotypes with equal arithmetic and geometric mean fitnesses. Expressing the same phenotype each year should give the same fitness as expressing the two phenotypes in a fixed sequence (say, small eggs early, large eggs later). But with overlapping generations, the fixed-sequence tactic creates a situation in which older parents and their adult offspring tend to express different egg-size phenotypes, which lowers the variance experienced by the family (hence, genotype) as a whole. The fixed-sequence tactic may therefore be better than consistently expressing one phenotype, but given real-world population fluctuations, it probably
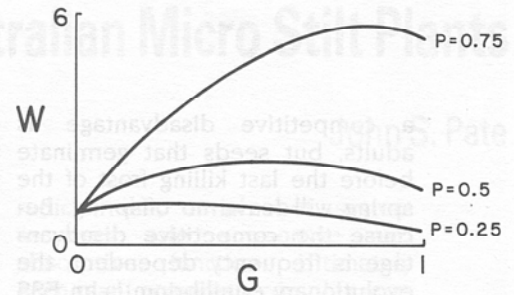

Fig. 1. Cohen's model for delayed germination in an annual plant.

A typical plant sets $Y_g = 20$ seeds in a good year and $Y_b = 0.1$ seed in a bad year. Seeds that do not germinate will survive to the next year with probability $s = 0.8$. Each curve shows the geometric mean fitness W achieved by seeds that germinate with probability G, for a given frequency of good years p. The maximum fitnesses occur at $G = 0.254$, $G = 0.551$ and $G = 0.847$, for $p = 0.25$, $p = 0.5$ and $p = 0.75$.

would not do as well as would producing the full range of offspring sizes within each clutch. To explain the parent–offspring size correlation as a bet-hedging tactic, one must explain why an increased level of within-clutch variation would not have achieved the same end in a simpler and more robust way. Other possible explanations for the correlation include non-adaptive allometric constraints[30] and extended versions of the Smith–Fretwell model in which clutches of different sizes are equivalent to environments with different optimal offspring sizes[31].

Et cetera

Many life-history phenomena are potentially subject to selection for either conservative or diversified bet-hedging. Cohen modelled the timing of growth and reproduction in a seasonal environment[32]. When favourable conditions end at a predictable time, the best tactic is to switch abruptly from growth to reproduction. But if the favourable growing season ends unpredictably, then relatively late flowering times may give the highest mean seed production, but at the cost of a greatly increased variance, owing to catastrophic failures when good conditions end early. Under such circumstances the best tactic may be conservative (flower earlier than would be necessary in an average year), or it may be diversified (grow and flower concurrently over an extended period of time).

Strategies for the timing of germination within a season can be extremely complicated[33,34]. Seeds that germinate late may have

a competitive disadvantage as adults, but seeds that germinate before the last killing frost of the spring will leave no offspring. Because the competitive disadvantage is frequency dependent, the evolutionary equilibrium is an ESS rather than a simple optimum. Depending on the size of the competitive advantage gained by early germination, and the shape of the probability distribution of last frosts, the solution may be for all seeds to germinate on a single conservative date or for seeds to germinate over a range of dates.

Washburn et al.[35] have recently described a spectacular phenotypic polymorphism in the ciliate protozoan *Lambornella clarki*, which may develop as either (i) a free-living form that feeds on bacteria and other microorganisms in water-filled treeholes, and is itself preyed on by larvae of the mosquito *Aedes sierrensis*, or (ii) a parasitic form that attacks and kills the mosquito larvae. The development of parasitic forms is induced by the presence of mosquito larvae, or by water previously conditioned by mosquito larvae; parasitic forms appear one to three days after free-living forms are first exposed to the stimulus. This transformation is a facultative response to a changed environment, not an instance of bet-hedging. But if free-living ciliates are *not* exposed either to mosquitoes or to conditioned water, a few of them none the less give rise to parasitic forms,

all of which die within 24 hours because they are irreversibly committed to parasitism. These parasitic forms would presumably enjoy a significant selective advantage over their free-living counterparts if mosquito larvae *did* appear during the brief time they can survive without hosts[36]. It is tempting to speculate that their rate of spontaneous development (in the absence of mosquitoes) is adjusted by selection to hedge bets against the probability that mosquitoes will soon arrive.

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