

Within-generation bet hedging: a seductive explanation?

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Bet hedging occurs when a single genotype shows a variety of phenotypes in the same environment, and each phenotype is successful only when the particular circumstances to which it is adapted occur. The time scale of between-generation bet hedging ensures that all individuals with a given phenotype suffer the same fate – circumstances such as drought exert homogenous pressure on all members of a population. Under within-generation bet hedging, however, individuals with the same phenotype are subject to heterogeneous selection pressure – predation, for example, will affect some individuals but not others. An important consequence of this difference is that conditions favoring the evolution of within-generation bet hedging are very restricted. While a single lineage may realize increased fitness via within-generation bet hedging, this fitness advantage varies inversely with population size and becomes vanishingly small at even modest population sizes. Although several reviews and analyses have highlighted the differences between these two types of bet hedging, confusion persists regarding their respective definitions and evolutionary justification. Bet hedging is a seductive explanation because most students of evolution are trained to focus on costs and benefits at the individual level, and tend to seek adaptive explanations for individual traits. Although this focus is often successful, it leads us astray in the case of within-generation bet hedging. Only by assessing the fitness effects of a trait in the context of whole populations can one accurately identify traits that can and cannot be favored by within-generation bet hedging.

Environmental unpredictability often acts to limit how well adapted organisms are to their environment. Because no single phenotype is optimal in all potentially occurring environments, bet hedging strategies can increase an organism's mean fitness by ensuring that some progeny will survive regardless of environmental conditions. In predictable environments, selection will act to produce a single best-adapted phenotype (e.g. heat tolerance in tropical climates). The environment, however, may change in unpredictable ways, sometimes favoring one phenotype, sometimes another. Where phenotypes are mutually exclusive (e.g. duration of obligate diapause), adaptation to one set of environmental conditions can preclude adaptation to another, unpredictably occurring, set of conditions. Under these

circumstances, bet hedging or risk spreading may evolve.

A common form of bet hedging occurs when a single genotype produces multiple phenotypes that are adapted to different selection regimes. Between-generation risk spreaders produce an assortment of progeny phenotypes each season, and each phenotype is successful only when the particular situation to which it is adapted occurs. Desert dwelling annual plants, for example, may produce several classes of seeds, each with a different dormancy duration (Cohen 1966). Because annual rainfall is unpredictable, a given phenotype (e.g. seeds that germinate in one season) may either be favored, in years when rainfall is high, or disfavored, in years when a killing drought occurs. Were all plants of a given genotype to bet their genetic resources on a single phenotype (e.g. germinate upon the arrival of spring), environmental extremes could lead to the extermination of all progeny. By producing seeds with multiple-dormancy phenotypes, individuals sharing a single seed-dormancy genotype can increase their mean fitness by ensuring that some seeds will survive regardless of environmental conditions.

In this example, all phenotypes will experience identical selection within a given season. Thus, single-season germinators produced in a drought will all die, while 2+ -season germinators may survive, depending upon conditions at the time when they exit dormancy. Within any one generation, genotypes producing the greatest number of adapted phenotypes will be most fit. Across multiple generations, however, selection will favor those genotypes whose allocation of progeny phenotypes best matches environmental conditions over time – in other words, those with the highest geometric mean fitness. For fitness values measured over n successive generations, the geometric mean is the n th root of the product of the n fitness values ($\mu_G = n\sqrt[n]{f_1 \times f_2 \times \dots \times f_n}$) (Dempster 1955). The fitness of such between-genera-

tion bet hedging genotypes depends only upon the arithmetic mean (μ_A) and variance (σ^2) in fitness, such that $\mu_G = \mu_A - \sigma^2/2$ (Gillespie 1974).

A second, more restricted, form of bet hedging occurs within generations. Here, different progeny phenotypes may not occur; instead, risk may be spread via the placement (temporal or spatial) of progeny. Butterflies, for example, may distribute their eggs over many more host plants than are required to support larval growth and development, in spite of the increased costs this entails (Root and Kareiva 1984). Progeny on any particular plant are subject to unpredictable disasters, such as the destruction of their host plant by large herbivores, which may eliminate all individuals on a plant.

Within-generation bet hedging evolves under a much narrower set of circumstances than between-generation bet hedging. Although several reviews and analyses have highlighted the differences between these two types of bet hedging (Gillespie 1973, 1976, Courtney 1986, Seger and Brockman 1987, Hopper 1999), confusion persists regarding their respective definitions and evolutionary justification. Furthermore, within-generation bet hedging continues to be invoked as an explanation in systems where it is unlikely to have evolved (Freese and Zwolfer 1996). For these reasons, we describe here as plainly as we can the distinguishing characteristics of within- and between-generation bet hedging.

Unlike between-generation bet hedging, within-generation bet hedging involves heterogeneity in the selection pressures to which a given phenotype is exposed. Consider between-generation bet hedging by desert plants: in a season of drought, all germinating seeds will be eliminated. Assessing the relative fitness of bet hedgers and non-bet hedgers is straightforward: if the germinating seeds are the progeny of a non-bet hedging genotype, lineage extinction occurs; if, instead, they are the progeny of a bet hedging genotype, the probability of extinction is far lower, since the risk of choosing an inappropriate germination date is spread over two or more seasons. This is in contrast to within-generation bet hedging by butterflies: some butterflies that lay all of their eggs on a single plant will realize zero fitness because the plant is destroyed by a vertebrate herbivore, but other individuals who adopt this strategy will lay all of their eggs on a plant that escapes destruction and so suffer no reduction in fitness. In short, not all within-generation bet hedgers with the same phenotype experience the same fate.

The most important difference between these two sorts of bet hedging is the effect of population size. For within-generation bet hedging, the fitness of a genotype over multiple generations depends on the arithmetic mean and variance in fitness (as is true for between-generation bet hedging), but is also strongly influenced by population size (m), such that $\mu_W = \mu_A - \sigma^2/m$, Gille-

spie 1974). Where the population of non-bet hedgers is large, the probability that all non-bet hedging lineages will be eliminated is quite small, even if the extinction probability of individual lineages is large: $P(\text{extinction of individual non-bet hedging lineage}) = P(\text{plant destruction})$; $P(\text{extinction of entire population of non-bet hedging lineages}) = P(\text{plant destruction})^m$. Thus, the effects of stochastically occurring risks are less pronounced in within-generation bet hedging, because the effects of variance are attenuated by population size (i.e. σ^2 is divided by population size, versus $\sigma^2/2$ for between-generation bet hedgers).

A more explicit discussion of within-generation bet hedging will perhaps serve to clarify the restrictive effects of heterogeneous selection pressure and population size on the evolution of this strategy. One of us (KRH) first became interested in bet hedging as a possible explanation for the oviposition patterns of parasitoid wasps attacking aphids. Female wasps consistently oviposit into fewer aphids than are available in a colony, instead spreading their eggs over aphids in multiple colonies. Aphid colonies, much like the host plants of butterflies, are subject to unpredictable catastrophes such as predation, which can eliminate entire colonies. Parasitoid oviposition patterns might thus be explained by within-generation bet hedging: by spreading their progeny among multiple colonies, female wasps may avoid losing them all when a colony is preyed upon.

Patterns such as this have intuitive appeal as examples of within-generation bet hedging, but explicit analysis reveals that selection for bet hedging is actually unlikely here. Mathematically, the benefits of within-generation bet hedging in the aphid/parasitoid system can be assessed as follows. If other sources of parasitoid mortality are equal, the fitness of an individual female would be the number of surviving progeny per aphid colony attacked (f) times the number of aphid colonies not destroyed by predation (n). If predation is random, then the probability of colony survival (p) is the same for all colonies, and n will have a binomial distribution with mean $E[n] = Np$ and variance $V[n] = Np(1-p)$ (Feller 1950), where N is the number of aphid colonies into which a wasp oviposits. Assume that each female produces 1.2 progeny when predation is absent, so that $f = 1.2/N$ (i.e. progeny per colony = total progeny/number colonies over which progeny are distributed) and, further, that $p = 0.9$. With these values in hand, the arithmetic mean fitness of a non-bet hedging female ($N = 1$) can be described as $\mu_A = fNp = 1.2 \times 1 \times 0.9 = 1.08$; the variance in fitness is $V[fN] = f^2 Np(1-p) = 1.2^2 \times 1 \times 0.9 \times 0.1 = 0.13$; and the fitness of a single lineage ($m = 1$) over multiple generations is $\mu_W = \mu_A - \sigma^2/m = 1.08 - (0.13/1) = 0.95$. More realistically, consider the mean fitness of non-bet hedgers when $m = 100$ non-bet hedging lineages: in this case, $\mu_G = \mu_A - \sigma^2/m = 1.08 - (0.13/$

Table 1. Comparison of across-generation fitness values for individual lineages ($m = 1$) and entire populations ($m = 100$) of non-bet hedging and within-generation bet hedging aphid parasitoids where the probability of an aphid colony and associated parasitoid progeny experiencing catastrophic predation is either 10% ($p = 0.9$) or 50% ($p = 0.5$)

m	Non-bet hedgers			Bet hedgers		
	1	100	100	1	100	100
p	0.9	0.9	0.5	0.9	0.9	0.5
μ_A	1.08	1.08	0.6	1.08	1.08	0.6
σ^2	0.13	0.13	0.36	0.013	0.013	0.036
μ_G	0.95	1.0787	0.5964	1.067	1.0799	0.5996

100) = 1.0787. Changing the selection pressure by setting $p = 0.5$ (i.e. only 50% of all aphid colonies escape predation) results in $\mu_A = 1.2 \times 1 \times 0.5 = 0.6$; $V[fn] = 1.2^2 \times 1 \times 0.5 \times 0.5 = 0.36$; and $\mu_G = 0.6 - (0.36/100) = 0.5964$.

For bet hedging females, assume that each female distributes her progeny over 10 aphid colonies ($N = 10$; $f = 1.2/10 = 0.12$). Thus, $\mu_A = 0.12 \times 10 \times 0.9 = 1.08$; $V[fn] = 0.12^2 \times 10 \times 0.9 \times 0.1 = 0.013$; and the mean fitness of a single lineage ($m = 1$) is $\mu_W = 1.08 - (0.013/10) = 1.067$. For a population of 100 bet hedging lineages, $\mu_W = 1.08 - (0.013/100) = 1.0799$. When $p = 0.5$, $\mu_A = 0.12 \times 10 \times 0.5 = 0.6$; $V[fn] = 0.12^2 \times 10 \times 0.5 \times 0.5 = 0.036$; and $\mu_W = 0.6 - (0.036/100) = 0.5996$.

As is clear in Table 1, consideration of the effects of population size is crucial for assessing the fitness advantage of within-generation bet hedgers over non-bet hedgers. Even at modest population sizes, the relative increase in fitness due to within-generation bet hedging is vanishingly small, and adjusting the frequency of catastrophic destruction of aphid colonies (i.e. increasing the strength of selection against non-bet hedgers) has very little effect. Furthermore, bet hedging in nature almost always has a cost (Roitberg et al. 1999), further decreasing the success of within-generation bet hedgers. For large populations (e.g. most insect populations) within-generation bet hedging will offer very little advantage, and is likely to be outweighed by associated costs.

Why, a full quarter century after within-generation bet hedging was elucidated by Gillespie (1973, 1974, 1975, 1976), and in the face of exhaustive reviews of bet hedging (Seeger and Brockman 1987, Yasui 1998, Hopper 1999), does within-generation bet hedging continue to be invoked in such an erroneous manner? We believe that two factors contribute to the appeal of within-generation bet hedging as an explanation for biological phenomena. The first of these is the axiom that natural selection acts upon individuals rather than on populations. Most students of evolution are trained to focus on the costs and benefits of traits at the level of the individual (Grafen 1999). This approach, though correct and generally successful, leads us astray in the case of within-generation bet hedging: a strategy that is risky for an isolated individual (e.g. a single, non-bet hedging aphid parasitoid) may have no appreciable effect on fitness when populations are large and the “risky”

strategy is widespread. The second component of within-generation bet hedging’s explanatory appeal is more subtle: as evolutionary biologists we are frequently impressed by the ability of organisms to adapt to their environment. Thus, when faced with traits that do not appear to increase fitness, we instinctively seek adaptive explanations. Not all adaptations are obvious, however, and our failure to discover an evolutionary justification for a trait does not imply that none exists. Moreover, behaviors with nearly neutral effects on fitness can persist, even when more adaptive alternatives exist.

Because of its superficial concordance with evolutionary dogma, the siren song of within-generation bet hedging is unlikely to “softly and suddenly vanish away/and never be met with again,” (Carroll 1875). By focusing attention on the fitness effects of a trait in the context of whole populations, however, we hope to render the task of distinguishing those traits that can be favored by bet hedging from those which cannot far more straightforward.

References

- Carroll, L (C. L. Dodgson). 1875. The hunting of the snark. – In: K. Silver (ed.), Lewis Carroll Selected Poems. 1995. Carcanet Press, Manchester, UK.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. – *J. Theor. Biol.* 12: 119–129.
- Courtney, S. P. 1986. Why insects move between host patches: some comments on ‘risk-spreading’. – *Oikos* 47: 112–114.
- Dempster, E. R. 1955. Maintenance of genetic heterogeneity. – *Cold Spring Harbor Symp. Quantitative Biol.* 20: 25–32.
- Feller, W. 1950. An introduction to probability theory and its applications. – Wiley.
- Freese, G. and Zwolfer, H. 1996. The problem of optimal clutch size in a tritrophic system: the oviposition strategy of the thistle gallfly *Urophora cardui* (Diptera, Tephritidae). – *Oecologia* 108: 293–302.
- Gillespie, J. H. 1973. Natural selection with varying selection coefficients – a haploid model. – *Genet. Res.* 21: 115–120.
- Gillespie, J. H. 1974. Natural selection for within-generation variance in offspring number. – *Genetics* 76: 601–606.
- Gillespie, J. H. 1975. Natural selection for within-generation variance in offspring number II. discrete haploid models. – *Genetics* 81: 403–413.
- Gillespie, J. H. 1976. Natural selection for variances in offspring numbers: a new evolutionary principle. – *Am. Nat.* 111: 1010–1014.
- Grafen, A. 1999. Formal Darwinism, the individual-as-maximizing-agent analogy and bet-hedging. – *Proc. R. Soc. Lond. B* 266: 799–803.

- Hopper, K. R. 1999. Risk-spreading and bet-hedging in insect population biology. – *Annu. Rev. Entomol.* 44: 535–560.
- Roitberg, B. D., Robertson, I. C. and Tyerman, J. G. A. 1999. Vive la variance: a functional oviposition theory for insect herbivores. – *Entomol. Exp. Appl.* 91: 187–194.
- Root, R. B. and Kareiva, P. M. 1984. The search for resources by cabbage butterflies (*Pieris rapae*): ecological consequences and adaptive significance of Markovian movements in a patchy environments. – *Ecology* 65: 147–165.
- Seger, J. and Brockman, H. J. 1987. What is bet-hedging? – In: Harvey, P. H and Partridge, L (eds), *Oxford Surveys in Evolutionary Biology*. Vol. 4. Oxford Univ. Press, pp. 182–211.
- Yasui, Y. 1998. The ‘genetic benefits’ of female multiple mating reconsidered. – *Trends Ecol. Evol.* 13: 246–250.