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NOTE

Unifying Within- and Between-Generation Bet-Hedging Theories: An Ode to J. H. Gillespie

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ABSTRACT: In the 1970s, John Gillespie introduced two principles in which evolution selects for genotypes with lower variation in offspring numbers. First, if the variation in offspring number primarily occurs within generations, the strength of this selective force is inversely proportional to population size. Second, if this variation primarily occurs between generations, the strength of this selective force is proportional to the variance and independent of population size. These principles lie at the core of bet-hedging theory. Using the common currency of fixation probabilities, I derive a general principle for which within-generation correlation of individual fitness acts as a dial between Gillespie's limiting cases. At low correlations, within-generation variation is the primary selective force. At high correlations, between-generation variation is the dominant selective force. As corollary of this general principle, selection for diversified bet-hedging strategies is shown to require higher within-generation environmental correlations in smaller populations.

Keywords: bet hedging, stochastic life history, fixation probabilities.

Introduction

Populations exhibit variation in fitness at multiple scales. Across generations, environmental conditions may fluctuate and, thereby, generate temporal fluctuations in the mean fitness of the population. Within generations, individual fitness varies about this mean as a result of chance events or within-generation environmental variation experienced by individuals. All else being equal, natural selection can favor genotypes that reduce this variation. When this reduction occurs at the expense of mean fitness, evolutionary bet hedging has occurred (Childs et al. 2010; Simons 2011). For both sources of variability, Gillespie (1973, 1974) demonstrated this evolutionary principle by using diffusion approximations. For infinitely large populations experiencing only temporal variation in fitness, Gillespie (1973) demonstrated that there is selection for the genotype with the higher value of

$$\mu_i - \frac{\tau_i^2}{2}, \tag{1}$$

where μ_i (close to 1) is the average number of offspring for genotype i and τ_i^2 is the between-generation variance in the number of offspring. Alternatively, for finite populations of size N experiencing only within-generation variation in offspring numbers, Gillespie (1974) showed that there is selection for the higher value of

$$\mu_i - \frac{\sigma_i^2}{N}, \tag{2}$$

where σ_i^2 is the within-generation variance in the number of offspring. Using the common currency of fixation probabilities (Proulx and Day 2002), I introduce a long-term fitness metric that includes equations (1) and (2) and more recent work by Starrfelt and Kokko (2012) as special limiting cases.

The wet-dry scenario. To motivate the main result, I consider an example from Starrfelt and Kokko (2012) in which each individual within a population experiences either a wet or a dry environment throughout its lifetime. The number of offspring produced by each individual depends on its genotype and whether it experienced a wet or a dry environment. There are three genotypes: a drought-resistant genotype that is a dry-environment specialist (A_{dry}), a wet-environment specialist (A_{wet}), and a diversified genotype that gives rise to both wet- and dry-environment specialist phenotypes (A_{div}). All genotypes are haploid and reproduce asexually without mutation. Consequently, like begets like for the specialist genotypes. For the diversified genotype, a fixed fraction of the offspring of each individual are phenotypically wet-specialists throughout their lifetime, and the remaining fraction are dry-specialists. After reproduction, there is global population regulation maintaining

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a total population size of N, for example, lottery competition among the offspring for N occupiable sites. Hence, the competing genotypes experience hard selection (Wallace 1975).

Consistent with Starrfelt and Kokko (2012), I assume that the specialists experiencing their preferred environment conditions have an equal number of offspring. Table 1 reports fitness values (offspring numbers) for all genotypes normalized so that the maximal value is 1; for example, if the number of offspring produced by the specialists experiencing their preferred environment conditions is 100, then a value of 0.6 corresponds to 60 offspring. In dry environments, dry- and wet-specialists have fitnesses 1.0 and 0.6, respectively. In wet environments, dry- and wet-specialists have fitnesses 0.55 and 1.0, respectively. For the diversified genotype, 25% of the individuals are dry-specialists throughout their lifetime, and the remaining 75% are wet-specialists. Hence, the expected fitness of a randomly chosen diversified individual is $0.25 \times 1 + 0.75 \times 0.6 = 0.7$ in a dry environment and $0.25 \times 0.55 + 0.75 \times 1 = 0.8875$ in a wet environment. As shown below, the fractions 25% and 75% were chosen to favor the diversified genotype in a temporally fluctuating environment (see also fig. 1).

Suppose the source of environmental heterogeneity is purely spatial. Each year, each individual has a 50% chance of experiencing a dry environment throughout its lifetime and a 50% chance of experiencing a wet environment throughout its lifetime. Hence, the expected fitness μ_i is $0.5 \times 1 + 0.5 \times 0.55 = 0.775$ for a randomly chosen dry-specialist, $0.5 \times 0.6 + 0.5 \times 1 = 0.8$ for a randomly chosen wet-specialist, and $0.25 \times 0.775 + 0.75 \times 0.8 = 0.79375$ for a randomly chosen individual of the diversified genotype. Moreover, the variances in the number of offspring are $\sigma_i^2 = 0.5 \times (1-0.775)^2 + 0.5 \times (0.55 - 0.775)^2 \approx 0.051$ for the dry-specialists, $\sigma_i^2 = 0.5 \times (1 - 0.8)^2 + 0.5 \times (0.6 - 0.8)^2 = 0.04$ for the wet-specialists, and $\sigma_i^2 = 0.5 \times (1 - 0.79375)^2 + 0.75 \times 0.5 \times (0.6 - 0.79375)^2 + 0.25 \times 0.5 \times (0.55 - 0.79375)^2 \approx 0.043$ for the diversified genotype. Since there is only within-generation variation in the offspring number, equation (2) is the appropriate long-term fitness metric. As the wet-specialist genotype has both the highest mean and the lowest variance, natural selection favors this specialist at all population sizes.

Next, imagine that the source of environmental heterogeneity is purely temporal. Each year, there is a 50% chance that all individuals experience a dry environment, else all individuals experience a wet environment. Since there is only between-generation variation in the offspring number, equation (1) is the appropriate long-term fitness metric, provided that N is infinitely large. Averaging across years, the expected fitnesses of all the genotypes are as in the spatial case. Unlike the spatial case, however, the variances τ_i^2 in equation (1) correspond to the variation across years in the average fitness of a genotype. For the specialist genotypes, this distinction is inconsequential, as all individuals in a given year have the same number of offspring. Hence, $\tau_i^2 = \sigma_i^2$ are 0.051 and 0.04 for the dry- and wet-specialist genotypes, respectively. For the diversified genotype, however, the average fitness of an individual in a wet year is $0.25 \times 0.55 + 0.75 \times 1 = 0.8875$, while it is $0.25 \times 1 + 0.75 \times 0.6 = 0.7$ in a dry year. Therefore, $\tau_i^2 = 0.5 \times (0.8875 - 0.79375)^2 + 0.5 \times (0.7 - 0.79375)^2 \approx 0.009 < \sigma_i^2 = 0.043$, so that the diversified genotype significantly exhibits less variability in fitness across years than the specialist genotypes. As this reduction in variance results in $\mu_i - \tau_i^2/2 = 0.789$ for the diversified genotype but no change ($\mu_i - \tau_i^2/2 = 0.78$) for the wet-specialist genotype, natural selection favors the diversified genotype.

The two wet-dry environment scenarios demonstrate that the within- and between-generation variability can select for different genotypes. This observation raises two questions. For what mixture of spatial and temporal variability is there selection for the dry-specialist versus the diversified genotype? How might this answer depend on the population size N? To answer these questions, I derive a common fitness metric, using fixation probabilities for Wright-Fisher-type models.

Table 1: Arithmetic means and variances of fitness for the wet-dry scenario

	A_{dry}	A_{wet}	A_{div}[a]
Fitness in dry environment (50%)	1.0	.6	.7
Fitness in wet environment (50%)	.55	1.0	.887
Arithmetic mean μ_i	.775	.8	.794
Spatial variance σ_i^2	.051	.04	.043
Temporal variance τ_i^2	.051	.04	.009

Note: Randomly chosen individuals have a 50% chance of experiencing a wet environment and a 50% chance of experiencing a dry environment; 75% of diversified genotypes are wet specialists, and 25% are dry specialists.

[a] Randomly chosen individual of these genotypes.

Methods and Results

The Wright-Fisher-type model involves a population of N individuals consisting of two competing haploid genotypes, genotype 1 and genotype 2. Let μ_i be the expected number of offspring produced by individuals of genotype i, where this expectation is taken across space and time. Let η_i^2 be the net variance in this offspring number of genotype i across all individuals in space and time. Let ρ_i be the correlation in offspring number between two randomly chosen individuals without replacement of genotype i from the same generation. This ρ_i slightly differs from the correlation coefficients of Frank and Slatkin (1990) and Starrfelt

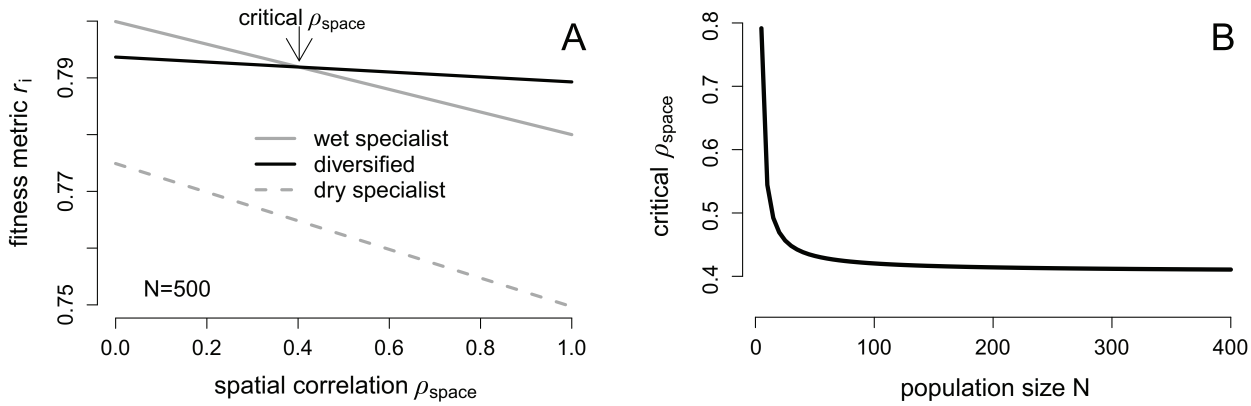

Figure 1: *A*, Fitness metric for the three genotypes as a function of the spatial environmental correlation. *B*, Critical spatial correlation that selects for diversified genotype.

and Kokko (2012), who considered the correlation between two randomly chosen individuals with replacement. While this difference is subtle, the definition used here naturally excludes correlations of individuals with themselves and, consequently, yields simpler formulas. As with the wet-dry scenario, the populations experience global regulation in which only N offspring enter the next generation to reproduce.

Under suitable assumptions (see appendix, available online), the genotype with the higher value of

$$r_i := \mu_i - \frac{\rho_i \eta_i^2}{2} - \frac{(1-\rho_i)\eta_i^2}{N} \tag{3}$$

has a fixation probability that is much higher when at low frequencies than that of the other genotype when it is at low frequencies. Specifically, when $r_2 > r_1$ and there is a single individual of genotype 2, the fixation probability of genotype 2 is approximated by

$$2\frac{r_2 - r_1}{(1-\rho_2)\eta_2^2}.$$

On the other hand, when $r_2 > r_1$ and there is a single individual of genotype 1, the probability of fixation of genotype 1 is effectively 0. This strong bias in the fixation probabilities suggests that genotypes with the higher value of r_i will tend to displace those with lower values of r_i. Consequently, r_i may be viewed as the long-term fitness of genotype i (see Proulx and Day 2002 for further discussion of the use of fixation probabilities as a long-term fitness metric).

From the fitness metric r_i, prior results about the separate effects of within- and between-generation variation on long-term evolution follow. When there are no within-generation correlations among individuals (i.e., $\rho_i = 0$ for both genotypes), equation (3) recovers Gillespie's (1974) result: natural selection favors the genotype with the higher value of $r_i = \mu_i - \eta_i^2/N$, where $\sigma_i^2 = \eta_i^2$. Alternatively, when individuals exhibit perfect within-generation correlations (i.e., $\rho_i = 1$ for both genotypes), equation (3) recovers Gillespie's (1973) result: natural selection favors the genotype with the higher value of $r_i = \mu_i - \eta_i^2/2$, where $\tau_i^2 = \eta_i^2$. Finally, when population sizes are infinite, equation (3) recovers Gillespie's (1973) result: natural selection favors the genotype with the higher value of $r_i = \mu_i - \rho_i\eta_i^2/2$. That is, weaker correlations among individuals reduce between-generation variation in fitness and, consequently, reduce selection for bet hedging in large populations.

Revisiting the wet-dry scenario. To get a better sense of what all this means, I revisit the case of wet-specialists, dry-specialists, and diversified genotypes. I assume that a randomly chosen individual across space and time has 50% chance of having experienced a wet environment and a 50% chance of having experienced a dry environment. In any given year, let ρ_{space} be the correlation in environmental conditions experienced by two randomly chosen individuals. When there are no spatial correlations (i.e., $\rho_{\text{space}} = 0$), 50% of individuals in each year experience a dry environment and 50% experience a wet environment (i.e., the purely spatial scenario from above). When all individuals experience the same environment within a given year (i.e., $\rho_{\text{space}} = 1$), 50% of the years are wet for all individuals and 50% of the years are dry for everyone (i.e., the purely temporal scenario from earlier).

For any degree of spatial correlation, the variations in the offspring number (η_i^2) across all individuals in space and time are $\eta_i^2 = 0.051$, 0.04, and 0.043 for the dry-specialist, wet-specialist, and diversified genotypes, respectively. For the specialist genotypes, the within-generation correlation ρ_i in offspring number simply equals the spatial correlation ρ_{space}. For the diversified genotype, however, the within-generation correlation increases linearly with ρ_{space} from 0 in spatially uncorrelated environments to 0.205 in perfectly spatially correlated environments. Consequently, when the environmental variation is purely temporal (i.e., $\rho_{\text{space}} = 1$), $\rho_i \eta_i^2 \approx 0.09 \approx \tau_i^2$ for the diversified genotype, as computed above. It is this lower value of ρ_i that favors the diversified genotype (Starrfelt and Kokko 2012).

For a population size of $N = 500$, figure 1*A* illustrates how the fitness metric r_i varies with the spatial correlation ρ_{space} for the three genotypes. As the long-term fitness of the specialist genotypes decreases more rapidly with spatial correlations than the long-term fitness of the diversified genotype, there is a critical value of ρ_{space}, ≈0.4, below which there is selection for the wet-specialist genotype and above which there is the selection for the diversified genotype. Figure 1*B* illustrates that this critical value of ρ_{space} decreases with the population size N. To understand why, recall that the wet-specialist genotype has two advantages over the diversified genotype: a higher μ_i value and a lower η_i^2/N value. While the first advantage is equally potent at all population sizes, the second advantage decreases with population size. Hence, for larger populations, the diversified genotype is favored in environments with lower spatial correlations.

Concluding Remarks

I introduced a long-term fitness metric r_i that plays a role in determining long-term evolutionary outcomes. By using the common currency of fixation probabilities, this metric realizes Starrfelt and Kokko's (2012, p. 742) vision that "within- and between-generation bet-hedging . . . can . . . be seen as two ends of a different continuum" and, thereby, unifies Gillespie's "new evolutionary principle" for which "the adaptive significance of a number of life-history strategies can be understood only when proper attention is paid to the variance component in offspring number" (Gillespie 1977, p. 1013).

This fitness metric highlights that within-generation correlations act as a dial along the within- and between-generation variation continuum. In the absence of within-generation correlations, the evolutionary importance of variation in offspring number is inversely proportional to the population size, and selection for bet hedging is more likely in smaller populations. In contrast, when all individuals have the same number of offspring within each generation, the evolutionary importance of variation in offspring number is independent of population size. All else being equal for any reasonably sized population (i.e., $N > 2$), selection for bet hedging is more likely with higher within-generation correlations.

Within-generation correlations in offspring number tend to increase with spatial correlations in environmental conditions. By having individuals that respond differentially to the same environment conditions, diversified genotypes can ensure that within-generation correlations remain low even in highly spatially correlated environments. This selective advantage, however, attenuates at smaller population sizes. Hence, all else being equal, selection for diversified bet hedging requires greater spatial correlations in smaller populations than in larger populations.

As all of the quantities described can be computed from multigeneration studies keeping track of individual fitness and total population size, this fitness metric r_i provides a means to empirically evaluate the relative contributions of within- and between-generation variation to long-term fitness and, ultimately, to evolutionary bet hedging. Confronting this theory with empirical data, however, is likely to highlight future theoretical challenges such as accounting for fluctuating population sizes; population structure in space, size, or age; and frequency- and density-dependent feedbacks.

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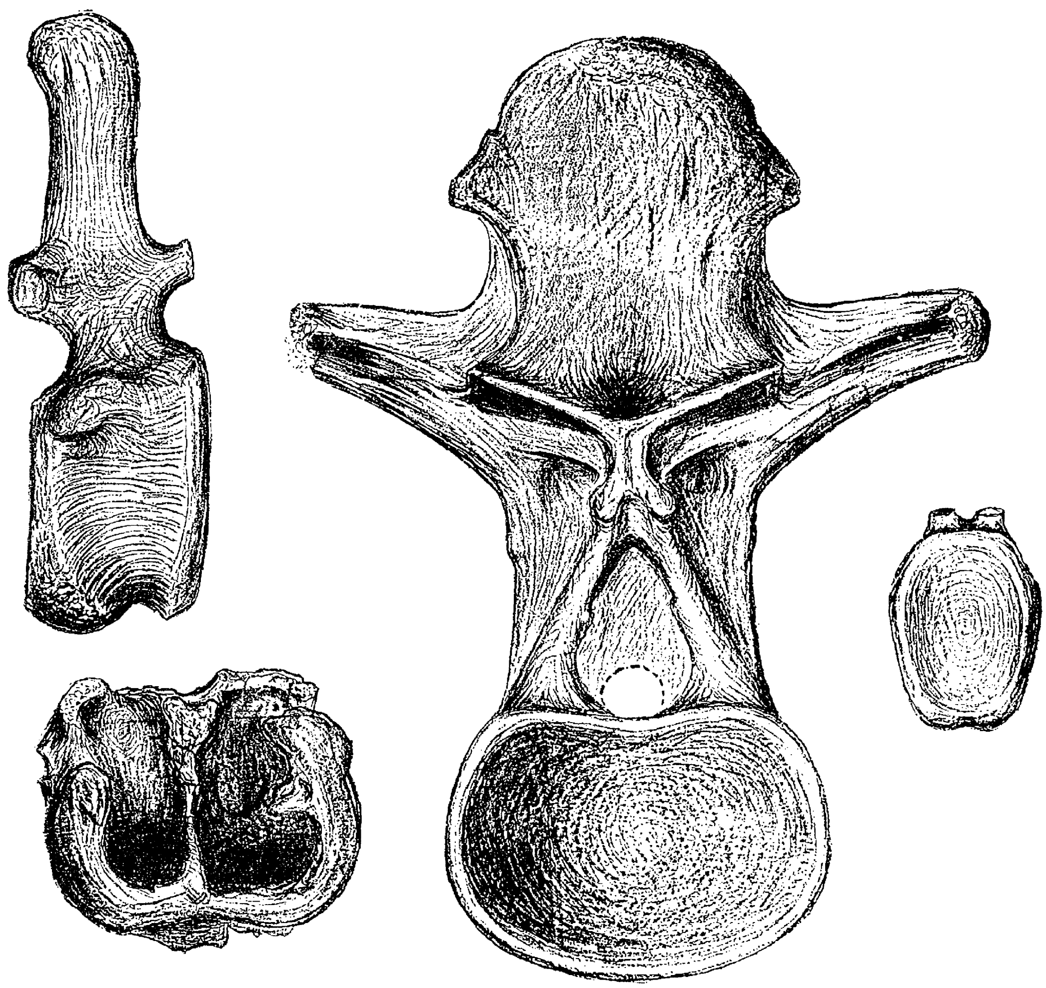

"As a shore and shallow water formation, the Dakota should enclose the remains of the plants and animals of the land . . . but vertebrate remains were until recently unknown. . . . It was therefore a source of no small gratification to have been in receipt of letters from Superintendent O. W. Lucas, of Canyon City, and Professor Arthur Lakes, of Morrison (both in Colorado and one hundred miles apart), at about the same time, informing me of their simultaneous discoveries of vertebrate remains in the beds of Dakota age, near their respective residences." From "On the Saurians Recently Discovered in the Dakota Beds of Colorado" by E. D. Cope (*The American Naturalist*, 1878, 12:71–85).