

Chapter 7

Integrated solutions to environmental heterogeneity: theory of multimoment reaction norms

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Environmental Heterogeneity

Environmental change drives evolution. If environments were constant, evolution rapidly would proceed to a rather humdrum, mostly static, equilibrium. The diversity of life we see today is the result of moderate but continual environmental challenges. Put simply, the seed of creation is the strife of organisms at odds with their changing environments. The premise of this book is that environmental variation is responsible for a spectacular suite of adaptations more intricate and labile than those for dealing with fixed environments. Phenotypic plasticity is one of those adaptations, but several others exist.

Among the many adaptations organisms have to cope with environmental variability are: dormancy (i.e., seedbanking or diapausing) to outlast problem environments; plasticity to produce relatively fit phenotypes for the demands of alternative environments; intermediate phenotypes (generalization) and bet-hedging, both of which reduce variance in performance across environments; and dispersal to leave when environments are unfavorable. Much theoretical literature addresses the merits of each strategy, generally as compared to ecological specialization (e.g., Levins 1968; Lewontin and Cohen 1969; Cohen 1976; Lively 1986a; Seger and Brockmann 1987; Van Tienderen 1997; reviewed in Wilson and Yoshimura 1994 and Chapter 6).

Traditionally, evolutionary ecologists define and contrast four strategies for coping with environmental heterogeneity. (1) Specialization: one phenotype is produced that is optimal for a given environment, even though the specialist may find itself sometimes in alternative environments. (2) Generalization: an intermediate, or otherwise general-purpose phenotype is produced, which is at least moderately successful in most environments. (3) Bet-hedging: an organism produces either (i) several phenotypes (e.g., among units in modular organisms or through producing diversified offspring) or (ii) single phenotypes probabilistically. (4) Phenotypic plasticity: environmental factors trigger production of alternative phenotypes. Other strategies are conceptually similar and can be considered as forms of these four. Strategies such as dormancy or iteroparity, for example, can be viewed as a type of temporal bet-hedging (Phillipi and Seger 1989). A generalized framework can accommodate all these possible strategies, such that each traditional strategy as well as additional strategies are special cases of the general construct.

The distinction between these strategies comes down to whether an organism adopts a single phenotype (specialists and generalists) or variable phenotypes (plasticity and bet-hedging). Plastic strategists produce variant phenotypes based on the nature of the environment, while bet-hedging strategists produce phenotypic variation within single environments. What is strategic about bet-hedging is that it reduces variance in fitness across generations, and hence increases geometric mean fitness (Dempster 1955; Lewontin and Cohen 1969). Many theorists also require

in their definition that bet-hedging reduce arithmetic mean fitness (Seger and Brockman 1987; Philippi and Seger 1989), but we see no need for, and do not adopt, this restriction.

Understanding how reduced variance in fitness across generations increases geometric mean fitness is core to the models we present, and central to all evolutionary thinking. The basic problem environmental variation presents is that it creates functional tradeoffs between environments, a pattern of selection known as divergent natural selection (DNS) (see Chapter 1). DNS is a problem for organisms because being equipped for one environment necessarily reduces performance in alternative environments. This type of tradeoff is represented graphically in Figure 7.1. In a given environment, a specialist (one who always produces the best phenotype for one of the environments) achieves maximum fitness in its specialized environment. Say that maximum is 10, and it has fitness of 2 in the alternative environment. If variation occurs within generations, we can calculate fitness simply by summing environment-specific fitnesses, weighted by environmental frequencies. If environments are equally frequent, the average fitness is 6 (i.e., $10 \times \frac{1}{2} + 2 \times \frac{1}{2}$). Note that a generalist producing an intermediate phenotype (with fitness 5 in either environment) has an average fitness of 5. If variation were between generations however, consider how these genotypes (and their subsequent lineages) do:

Specialist: $1 \times 10 \times 2 \times 10 \times 2 = 400$ progeny after four generations (average fitness = 6)

Generalist: $1 \times 5 \times 5 \times 5 \times 5 = 625$ progeny after four generations (average fitness = 5)

Bet-hedger: $1 \times 5 \times 6 \times 4 \times 5 = 600$ progeny after four generations (average fitness = 5)

Perfect plasticity: $1 \times 10 \times 10 \times 10 \times 10 = 10,000$ progeny after four generations

The clearest generality from this type of modeling is that plasticity, in the absence of constraints (i.e., perfect plasticity), is always the superior strategy in variable environments. The fact that plasticity is not ubiquitous (evident for all traits in all species) therefore suggests constraints are ubiquitous in natural systems (reviewed in DeWitt et al. 1998). First, plasticity may be costly (Van Tienderen 1991; Via et al. 1995). Alternatively, plasticity could be constrained by developmental range limits, where plasticity cannot produce phenotypic extremes (due to the need to retain flexibility) (DeWitt 1998). Another possibility, one that frequently has been modeled (Moran 1992; Getty 1996; Tufto 2000), is that plasticity is limited by accuracy of environmental cues used to guide development. Such constraints must be incorporated in any realistic model of the evolution of phenotypic plasticity.

Next we examine each of the traditional strategies (specialization, generalization, plasticity, and bet-hedging) and model integrated strategies that simultaneously combine elements of the foundational “pure” strategies. We evaluate whether integrated strategies provide better solutions to environmental heterogeneity than pure strategies. The goal is to find how closely each strategy approaches the ideal of perfect plasticity, given that certain constraints may be operating.

The Models

Following Levins (1962, 1968), the consequences of environmental shifts can be specified using a separate fitness function for each environment being modeled. Each fitness function describes the dependence of organismal performance (fitness) on phenotype for each specific environment. For simplicity, we use two environments in our models. Results from this simple scenario can easily be generalized, however, to environmental gradients or multiple categorical environments. When using only two environments, a fitness set is a useful way to summarize the fitness functions. For example, Figures 7.1a,b give two examples of fitness sets, with the component fitness functions specified in the top panel and the corresponding fitness sets mapped below. In the first scenario, fitness functions are highly overlapping and so produce a convex fitness set.

The second scenario involves only slightly overlapping fitness functions (i.e., strongly divergent selection) and so produces a concave fitness set. An intermediate amount of overlap in fitness functions results in a flat fitness set (not shown). In general, convex fitness sets favor generalists and concave sets favor specialization (Levins 1962, 1968). However, the exact outcome depends upon factors such as environmental frequencies, whether environmental variation occurs within or between generations, and whether fitness is frequency dependent. As these issues are trivial to the present goal, in the explicit models that follow we generally assume equally frequent environments, intergenerational variation, and no soft selection. However, the notation used allows for easy alteration of the first two assumptions.

Fitness functions define only the performance of a phenotype when in the specified environment. Calculating the actual fitness of genotypes must take into account (1) the probability of producing various phenotypes, (2) the frequency with which organisms experience each environment, and (3) whether alternative environments are encountered within single generations (fine-grained variation) or between generations (coarse-grained variation). Denoting the phenotype distribution produced by a genotype as $d(z; \mu_{ij}, \sigma_{ij})$, fitness within a generation is calculated by integrating the product of the phenotype distribution and fitness function (Yoshimura and Shields 1987, 1992, 1995):

$$w_j(\mu_{ij}, \sigma_{ij}) = \int f(z)_j \cdot d(z; \mu_{ij}, \sigma_{ij}) dz \quad (7.1)$$

where $w_j(\mu_{ij}, \sigma_{ij})$ is the fitness of genotype i in environment j . Fitness for the two environment case can be written for fine-grained variation as:

$$W(\mu_{ij}, \sigma_{ij}) = w(\mu_{i,j=1}, \sigma_{i,j=1}) \cdot p + w(\mu_{i,j=2}, \sigma_{i,j=2}) \cdot (1-p) \quad (7.2)$$

where p is the frequency of Environment 1 and $1-p$ is the frequency of Environment 2. For coarse-grained variation, the geometric mean is used to calculate fitness:

$$M(\mu_{ij}, \sigma_{ij}) = w(\mu_{i,j=1}, \sigma_{i,j=1})^p \cdot w(\mu_{i,j=2}, \sigma_{i,j=2})^{(1-p)} \quad (7.3)$$

It is important to emphasize for each of the above equations that each genotype produces an alternative phenotype density function with mean μ_i and standard deviation σ_i unique for each environment j . For the models that follow, we apply the above equations assuming intergenerational variation—parents and offspring may encounter different environments but in any given generation only one fitness function holds.

Strategies

Now we can define the strategies: (1) A specialist genotype produces only z_1^* , the optimum phenotype in Environment 1. (Optimal values are denoted by asterisks.) Note that an Environment 2 specialist is not defined to reduce redundancy. Since our fitness sets are symmetrical about their diagonal axis, specialists for Environments 1 and 2 are equivalent in terms of fitness. (2) A generalist genotype produces phenotypes intermediate between the fitness peaks for the two environments. (3) A plastic genotype produces phenotypes near z_1^* or z_2^* depending on its interpretation of environmental cues and other logistic constraints. (4) A bet-hedger genotype produces phenotypes probabilistically, with mean μ_i and variance σ_i^2 .

Traditionally the bet-hedging strategy involves adding variance around an intermediate phenotypic mean (i.e., a generalist who produces phenotypes probabilistically). However such variance could be added to any of the first three strategies. Thus we equate the term bet-hedging with variance per se and not with a singularly unique strategy unto itself. So we now have three

core strategies with bet-hedging being a possible attribute of each (box 7.1). Furthermore, the degree of bet-hedging (phenotypic variance) can differ across environments. While phenotypic plasticity produces different mean phenotypes across environments, it is perfectly conceivable that the magnitude of variance could also differ across environments. Thus we could define several synthetic strategies, such as a trait-mean specialist with plasticity for trait-variances (i.e., $\mu_{i,j=1} = \mu_{i,j=2}$, but $\sigma_{i,j=1} \neq \sigma_{i,j=2}$; box 7.1, column 3, rows 1 and 2).

Constraints on Plasticity

To model constraints on phenotypic plasticity, we simulated costs, developmental range limits, and varied reliability of cues. For each constraint, equation 7.3 was modified to reflect the unique nature of the constraint at hand:

$$M(\mu_i, \sigma_{ij}) = [w(\mu_{i,j=1}, \sigma_{i,j=1}) - C]^p \cdot [w(\mu_{i,j=2}, \sigma_{i,j=2}) - C]^{(1-p)} \quad (7.4)$$

$$M(\mu_i, \sigma_{ij}) = w[(\mu + L)_{i,j=1}, \sigma_{i,j=1}]^p \cdot w[(\mu - L)_{i,j=2}, \sigma_{i,j=2}]^{(1-p)} \quad (7.5)$$

$$M(\mu_i, \sigma_{ij}) = [w(\mu_{i,j=1}, \sigma_{i,j=1})^a \cdot w(\mu_{i,j=2}, \sigma_{i,j=2})^{(1-a)}]^p \cdot [w(\mu_{i,j=2}, \sigma_{i,j=2})^a \cdot w(\mu_{i,j=1}, \sigma_{i,j=1})^{(1-a)}]^{(1-p)} \quad (7.6)$$

In equation 7.4, C is the cost of plasticity. When C is zero this equation reduces to equation 7.3. This cost is assumed to be equal in both environments (Figure 7.1c), although this easily could be modified so that $C_1 \neq C_2$. L in equation 7.5 is the magnitude of developmental limits upon plasticity. Assuming $z_1^* < z_2^*$ (i.e., the fitness function for Environment 1 is to the left of that for Environment 2), L specifies the number of phenotype units by which the plastic genotype misses respective optima. If $z_1^* = 5$ and $z_2 = 10$, then a plastic strategist under $L=1$ would produce phenotypes of 6 and 9 respectively in Environments 1 and 2. Finally, equation 7.6 specifies the geometric mean fitness when plastic strategists are constrained by cue accuracy. The probability of the cue being accurate is represented by a and the probability of the cue signaling the wrong environment is $1-a$. Where the cue is completely reliable ($a = 1$) equation 7.6 reduces to equation 7.3. To more realistically reflect nature, we can specify environment-dependent cue accuracies ($a_1 \neq a_2$) in equation 7.6 to account for differences in reliability of cues between environments (see also Lively 1986a, 1999a; Moran 1991; Leon 1993; Getty 1996).

We proceed by modeling each strategy (i.e., those illustrated in box 7.1) under three fitness sets: concave (Figure 7.1a; $\sigma=1$), intermediate ($\sigma=2$), and convex (Figure 7.1b; $\sigma=3$). First, fitnesses of the purely deterministic strategies (box 7.1, first column) are compared. We additionally examine how pure generalization compares to plasticity with various constraints. Second, we evaluate bet-hedging strategies (box 7.1, second column). Finally, variance itself might be asymmetric across environments. Asymmetric (conditional) variance, as with simple (unconditional) bet-hedging, can be combined with any of the traditional pure strategies (box 7.1, third column). Strategies with asymmetrical variance are compared to those with symmetrical variance.

Computationally, the addition of bet-hedging to any pure strategy is achieved by adding a unique standard deviation σ to the phenotypic distribution for each genotype or genotype-environment combination. When testing effects of bet-hedging we varied σ from 0.5 to 6.

Model Outcomes

Pure Strategies

Under all fitness sets perfect plasticity was the optimal strategy. The relative fitness of specialists and generalists depends, as in previous models (reviewed in Wilson and Yoshimura 1994), on

the frequency of environments and structure of the fitness set. Assuming equal frequencies of the two environments and intergenerational variance, specialization always fails as a strategy relative to generalization. However, specialists do quantitatively better under convex fitness sets under our assumption of intergenerational variance. If environmental variance were intragenerational and the fitness set were concave, specialists would outcompete generalists. Yet, because specialists typically fail in our models, the interesting comparison is between the generalist and constrained plastic strategists.

Our model confirmed that the advantages of plasticity were greatest under concave fitness sets. In general, plasticity was fallible relative to generalists only under severe levels of two of the constraints (Figure 7.2). Furthermore, the nature of fitness differences between plasticity and generality depended on the constraint at hand (costs, developmental range limits, cue accuracy).

Costs: The structure of the fitness set had a large influence on the relationship of generalization and plasticity with costs (Figure 7.2a). We expressed costs of plasticity as a percentage fitness decline relative to perfect plasticity. Under a convex fitness set, a relatively low level of plasticity cost ($C = 29\%$) allowed generalists to beat plastic strategists. Under a concave fitness set, however, costs had to be particularly severe (i.e., $C = 96\%$) for generalists to beat plasticity. Generally, more divergent selection requires commensurately strong costs to prevent the evolution of plasticity.

Developmental range limits: Even extreme developmental range limits failed to lower the value of plasticity below that of generalization. That is, plastic strategists can be severely constrained by developmental range limits and still outperform generalists. The degree of superiority of plasticity depended on shape of the fitness set and degree of developmental limits (Figure 7.2b). Concave fitness sets resulted in an extreme advantage for plasticity even under high levels of constraint ($L < 80\%$). Plasticity's superiority was relatively modest under both convex and intermediate fitness sets.

Accuracy of cues: The advantage of plasticity over generalization increased with cue accuracy. The fitness of plastic strategists converged on that of generalists at 75% cue accuracy (i.e., 25% inaccuracy; Figure 7.2c). Interestingly, this effect was independent of fitness set shape and frequency of environments. As a consequence of using normal curves for fitness functions, this effect also remained invariant to changes in the individual fitness function breadths or peak locations, so long as the generalist produced a phenotype exactly between the peaks.

Strategies with Bet-hedging

Generally, both specialists and generalists benefited from some level of bet-hedging (Figure 7.3). The single exception was that generalists under convex fitness sets did not benefit from bet-hedging (Figure 7.3c). And if fitness sets were concave, a specialist with a small amount of bet-hedging ($\sigma = 1.14$ in our model) overcame pure generalization (Figure 7.3a). Bet-hedging decreased the fitness of unconstrained plasticity. Even when costs were imposed on plasticity bet-hedging awarded no benefits. So we tested to see whether plastic strategists constrained by developmental range limits and accuracy of cues could benefit by bet-hedging. To accomplish this, we invoked a given level of constraint and compared fitness of plastic strategists to strategists using plasticity and bet-hedging simultaneously.

Developmental range limits: When constrained by limits on phenotypic range, plastic strategists benefited from bet-hedging only under concave fitness sets. Furthermore, the optimal degree of bet-hedging increased with the magnitude of developmental limits (Figure 7.4). That is, the greater the developmental limits of plasticity the more bet-hedging is required to compensate for this limit.

Accuracy of cues: When environments were inscrutable, to any degree, plastic strategists benefited from bet-hedging. The optimal degree of bet-hedging increased as cues became increasingly flawed (Figure 7.5). Under intermediate and convex fitness sets, bet-hedging provided little benefit unless cues were very poor indicators of environmental conditions. Yet under a concave fitness set, even slight inaccuracy in cues (5% inaccuracy) made bet-hedging beneficial. Thus, just as with developmental range limits, cue inaccuracy required compensatory increases in the amount of bet-hedging.

Asymmetric Bet-hedging

Under assumptions that we have maintained so far (e.g., symmetrical fitness sets), only specialists gain from plasticity in trait variances (Figure 7.6a). Under a concave fitness set, specialists who produce no variance in their specialized environment but bet-hedge in their nonspecialized environment (i.e., “conditional bet-hedgers”) benefit greatly. Specialists with optimal asymmetric bet-hedging are 187 times more fit than pure specialists. Furthermore, this conditional strategy (bet-hedge only in the nonspecialized environment) increases fitness nearly twofold over the best symmetrical bet-hedge. Although generalists as we defined them do not benefit from asymmetric bet-hedging, they would if their phenotypic mean was not exactly intermediate between the two optimal phenotypes.

Just as unconstrained plastic strategists never benefited from bet-hedging, they failed to benefit from asymmetric bet-hedging. Furthermore, plastic strategists constrained by developmental range limits or cue inaccuracy failed to benefit more from asymmetric bet-hedging than from symmetric bet-hedging. However, if cue accuracy differed between environments, then asymmetric bet-hedging was beneficial (Figure 7.6b). Similarly, asymmetric bet-hedging provided fitness benefits when the developmental range limits differed by environment (not depicted).

Although the bulk of our modeling assumed symmetrical fitness sets, natural environments often differ in the shape of their fitness functions. In such cases asymmetric bet-hedging provided benefits to specialists, generalists, and constrained plastic strategists.

Integrated Strategies

An extensive literature compares specialization, generalization, bet-hedging, and phenotypic plasticity as evolutionary alternatives (reviewed in Wilson and Yoshimura 1994). Most of these papers demonstrate how certain factors (e.g., fitness set shape, habitat choice, density dependence, intergenerational environmental variance) favor one strategy over others. Rather than treat each foundational strategy as alternatives, our main result demonstrates integration of strategies as more often than not the optimal solution to environmental heterogeneity.

When comparing foundational strategies, our results concur with previous work. For example, pure generalists outcompete pure specialists given coarse-grained environmental variance, similar environmental frequencies and convex fitness sets. Also, perfect plasticity (i.e., assuming no constraints) is always optimal. However it is increasingly clear that perfect plasticity is uncommon in nature. Constraints on plasticity must exist. Either plasticity has costs or logistic difficulties that limit its efficacy (e.g., developmental range limits or inaccurate cues; DeWitt et al. 1998). In theory, these constraints need to be severe to prevent the evolution of plasticity (e.g., Van Tienderen 1991). Empirical studies also support this idea, as plasticity seems to have evolved despite the demonstration of potentially severe constraints (Langerhans and DeWitt 2002). Only under a limited range of conditions were generalists ever superior to constrained (costly or ignorant) plasticity (Figure 7.2a,c). Developmental range limits never

lowered fitness of plastic strategists below that of generalists (Figure 7.2b). Thus, among the pure (invariant within environment) strategies, plasticity is very hard to beat.

In our models, bet-hedging (adding variance, or noise, around phenotypic means) was generally a good thing. Perhaps most remarkably, specialists increased fitness through bet-hedging and even surpassed pure generalists when fitness sets were concave (Figure 7.3). Thus a specialist with a little noise can beat the traditional jack-of-all trades. However, a bet-hedging generalist (i.e., the traditional “bet-hedger” strategy) can always surpass a bet-hedging specialist. Bet-hedging generalists also surpass pure generalists under all but convex fitness sets.

When unconstrained or constrained only by costs, plastic strategists gained no advantages from bet-hedging. Yet when plasticity was constrained by developmental range limits or cue accuracy, integrating bet-hedging with plasticity proved beneficial, especially under concavity (Figures 7.4 and 7.5). As these two constraints increased in strength, the optimal magnitude of bet-hedging increased commensurately. So, under most conditions plasticity should integrate bet-hedging to optimize performance. Interestingly, one way to view the adaptive benefits of integrating strategies is that bet-hedging can compensate for limits of plasticity. This type of compensatory relationship, which is one way to create integrated adaptations, has been termed trait compensation (DeWitt et al. 1999).

In theory, asymmetric bet-hedging can be integrated with any of the foundational strategies (box 7.1, column 3). If the optimal variance changes across environments, we can expect the evolution of conditional bet-hedging. Specialists, in particular, stand to gain enormously through asymmetric bet-hedging. The optimal bet-hedging specialist produces no variance in its specialized environment and some optimal level of variance in its nonspecialized environment. This strategy can be termed plasticity for variance. Thus, both trait means and trait variances can exhibit reaction norms. This implies that we should expect to find interesting forms of plasticity where both trait means and variances differ across environments in manners that transcend simple mean-variance correlations (see below).

Although our standard model was structured with many symmetries (equal probability of alternative environments, symmetrical fitness functions, same-shape fitness functions for alternative environments, and exactly intermediate generalists), many of these assumptions will not hold in natural systems. Therefore some of these symmetries were relaxed to consider evolution under more realistic conditions. Of particular interest was that asymmetric bet-hedging provided benefits to plastic strategists if information reliability was greater in one environment than another ($a_1 \neq a_2$). Specifically, greater variance was favored in the more inscrutable environment. This may be a general phenomenon. Many plastic organisms experience either inducing or noninducing environments. Induction cues, when perceived, may more accurately reflect the true nature of the environment (i.e., reliably indicate the presence of the inducing agent) than failure to perceive a cue at all. For example, imagine a zooplankter that can chemically perceive planktivorous sunfish, but due to constraints of its sensory mechanism is unable to sense planktivorous minnows. In this case the sunfish cue informs the zooplankter with certainty that a planktivore is present, but the absence of a perceived cue could mean either no planktivores are present or minnows are present. Thus, it may be a general rule that less phenotypic variance (bet-hedging) occurs in inducing environments.

Conditional bet-hedging may turn out to be the rule in nature. Such a strategy should not only be selected by differentially reliable cues but also under many other situations. For example, asymmetric developmental range limits or asymmetric fitness sets would favor conditional bet-hedging. Likewise if the costs or logistic limits of canalization differed between environments, bet-hedging in the more constraining environment can compensate for plasticity’s limits.

A General Conceptual Framework for Evolution

So what represents the most complete (integrated) adaptive solution to naturally variable environments? We have stressed the need to think about plasticity in terms of trait means and trait variances. We also stressed that bet-hedging can be used to compensate for the limits of plasticity, thereby providing an optimal integrated solution to environmental variation. Yet we have only touched upon the breadth of possibilities with our models, expanding the usual strategy space from a four-box paradigm to a nine-box paradigm (box 7.1). Rather than limit our thinking to only nine boxes (based on the first two moments of phenotype distributions) however, it is possible to expand further. Quite likely skewness and other moments could be selected to differ in alternative environments. DeWitt and Yoshimura (1998) first suggested that higher moments of phenotype distributions may be under selection. And preliminary data has indicated this may be so (Weis and DeWitt, unpublished data). What we need to do now is assess whether the expanded paradigm—especially plasticity in higher moments of phenotype distributions—is of use for explaining the distribution and abundance of phenotypes in nature.

We believe the new view is important. To illustrate let us ask, “What would evolution look like in this new view?” We can make several predictions about the early course of population divergence. Assume an initially flat reaction norm for a population whose members have a moderate level of normally-distributed phenotypic variance within environments (Figure 7.7a). Now suppose divergent selection arises: the phenotypic optima shift below the norm in one environment and above the norm in the other environment. Selection will now simultaneously affect trait means, variances and higher moments, and the patterns for each moment will change as evolution proceeds. At first trait means and skewnesses will increase in the direction of the new optimum in each environment. Simultaneous with the mean and skewness changes, trait variance and kurtosis will increase in both environments (Figure 7.7b). As the reaction norm approaches the optima, variance and skewness will begin to decrease, and selection for trait-mean plasticity will continue. If perfect trait-mean plasticity is achieved, then all other moments should theoretically evolve to zero. Realistically however, some developmental noise will always persist (Figure 7.7c). Depending on the final constraints operating, some level of each moment may remain.

Concluding Remarks

In our theory of multimoment reaction norms, traditional strategies (specialist, generalist, bet-hedger, trait-mean plasticity) are special cases within a general strategy space. To maintain conditional strategies for multiple moments of phenotype distributions may at first seem unlikely, perhaps too sophisticated to expect. However this should be an empirical matter—we must look for such patterns where the functional ecology warrants.

Also, during the course of divergent natural selection it may be that shifts in trait means are accompanied by interesting and predictable evolutionary trajectories for higher moments of phenotype distributions (Figure 7.7). Thus the concept of multimoment reaction norms may be the most general conceptual framework for describing the strategy space of organisms in naturally variable environments.

Acknowledgments

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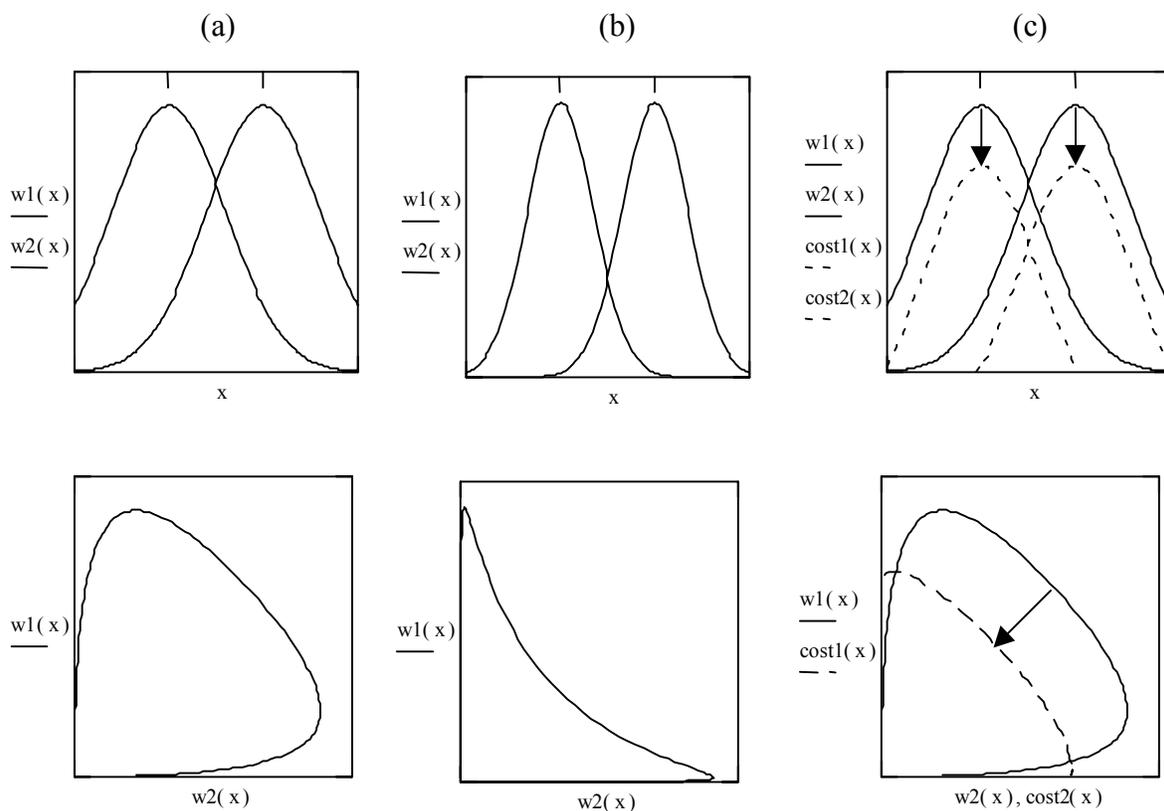


Figure 7.1. Fitness sets for the case of two environments. (a) Fitness functions (top panel) for two environments in which functions overlap broadly, producing a convex fitness set (bottom panel). (b) Slightly overlapping fitness functions (top) which produce a concave fitness set (bottom). (c) Fitness functions (solid lines) plus re-expressed functions with a value subtracted to represent the cost of phenotype production (dashed lines). When modeling costly plasticity, fitness for phenotypes produced through flexible development are taken from the dashed lines (following Leon 1991).

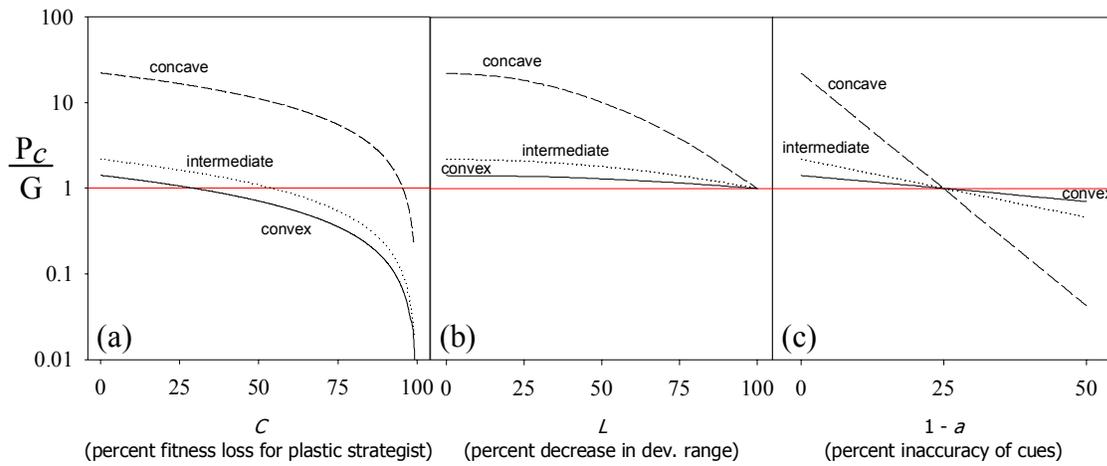


Figure 7.2. Fitness of plastic strategists relative to that of generalists under three types of constraint for three fitness sets. P_C / G = ratio of fitness for plasticity under a given constraint to generalization. (a) Costly plasticity. (b) Plasticity with limited developmental range. (c) Ignorant plasticity.

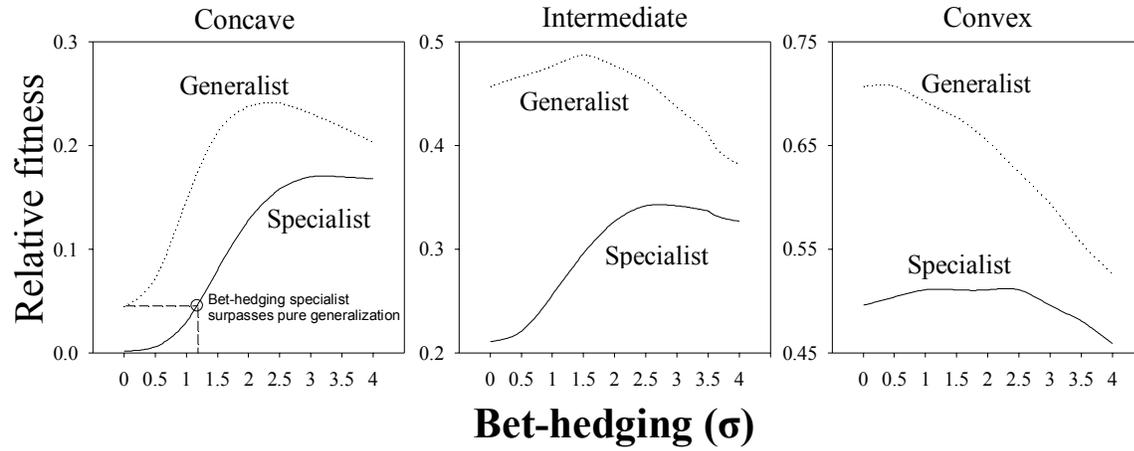


Figure 7.3. Fitness of bet-hedging specialists and generalists relative to perfect plasticity under three fitness sets. In the first panel we have indicated the level of bet-hedging at which specialists surpass fitness of pure (non-bet-hedging) generalists.

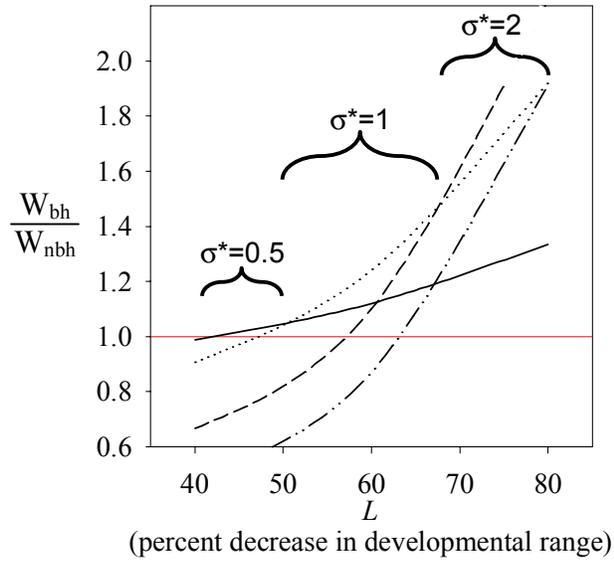


Figure 7.4. Fitness of bet-hedging plastic strategist relative to pure plastic strategists under varied developmental range limits. These results apply for the concave fitness set only; no benefits of bet-hedging were evident under intermediate or convex fitness sets. The optimal degree of bet-hedging (standard deviation of phenotypic mean) is depicted by σ^* . (—, $\sigma = 0.5$; ·····, $\sigma = 1$; - - - -, $\sigma = 2$; - · - ·, $\sigma = 3$). W_{bh} / W_{nbh} = ratio of fitness of bet-hedging plastic strategist to non-bet-hedging plastic strategist.

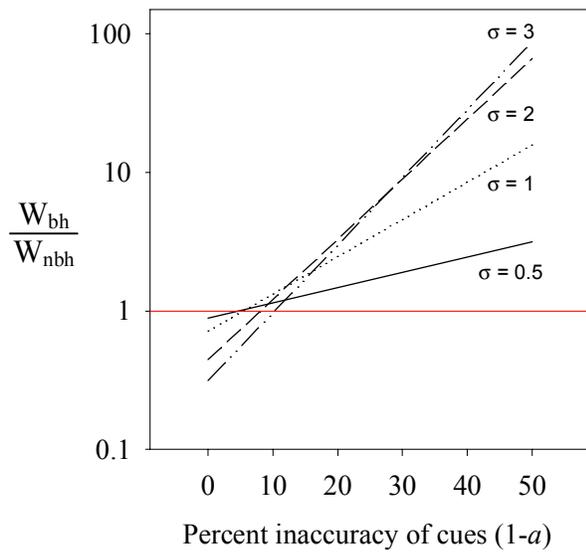


Figure 7.5. Fitness of bet-hedging plastic strategists constrained by inaccuracy of cues relative to pure plastic strategists. Depicted results apply for the concave fitness set. Minimal benefits of bet-hedging are awarded under intermediate and convex fitness sets. The optimal degree of bet-hedging (standard deviation of phenotypic mean) increased as inaccuracy of cues increased. W_{bh} / W_{nbh} = ratio of fitness of bet-hedging plastic strategist to non-bet-hedging plastic strategist.

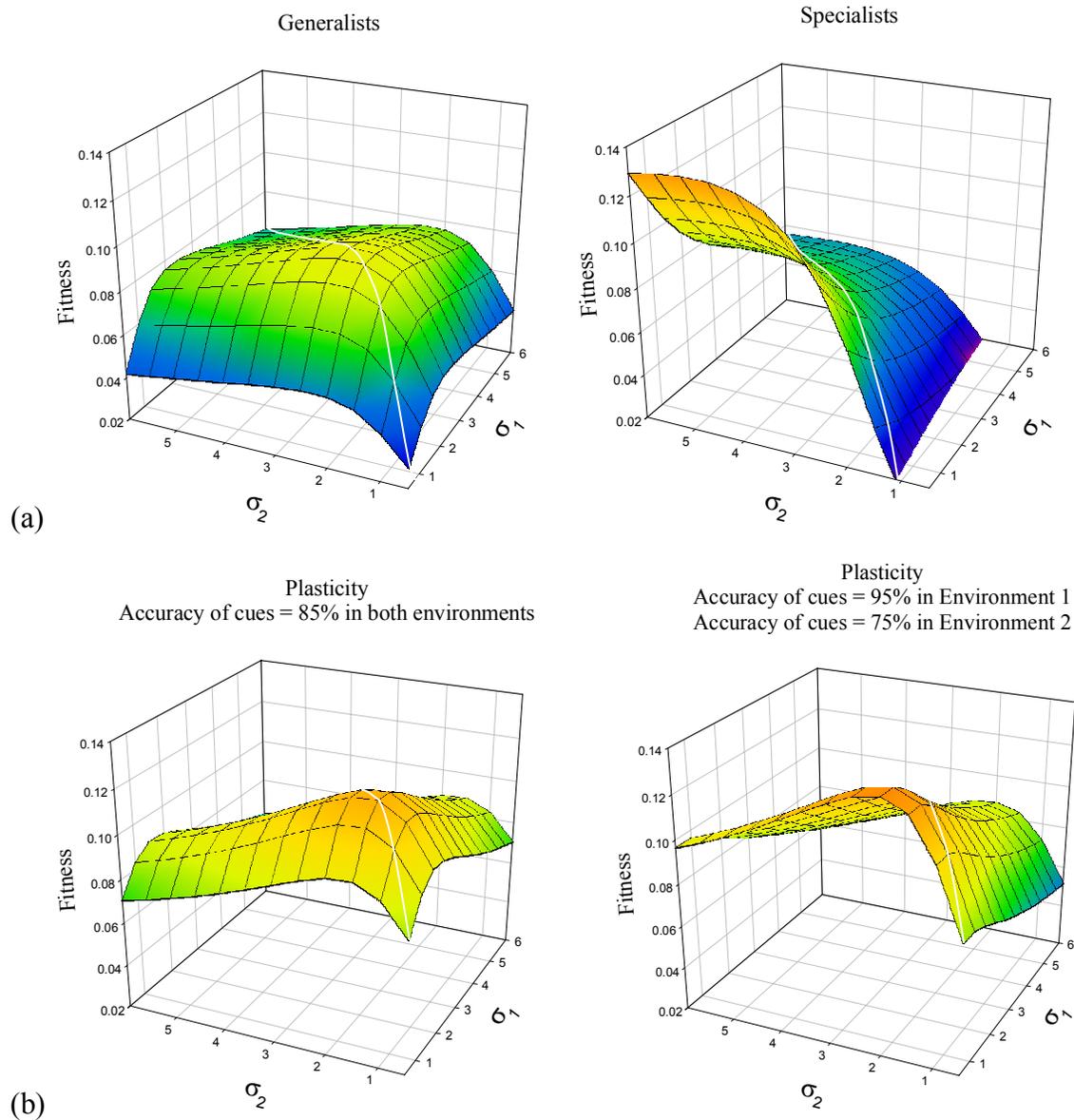


Figure 7.6. Fitness landscapes for variance in alternative environments under concave fitness sets (σ_i = standard deviation of phenotypes in alternative environments). The white line indicates symmetrical bet-hedging. (a) Symmetric bet-hedging is optimal for generalists (left panel), but *asymmetric* bet-hedging is optimal for specialists (right panel). (b) Symmetric bet-hedging is optimal when plasticity is equally constrained by cue accuracy in both environments (left panel). *Asymmetric* bet-hedging is optimal if cue accuracy differs for alternative environments (right panel).

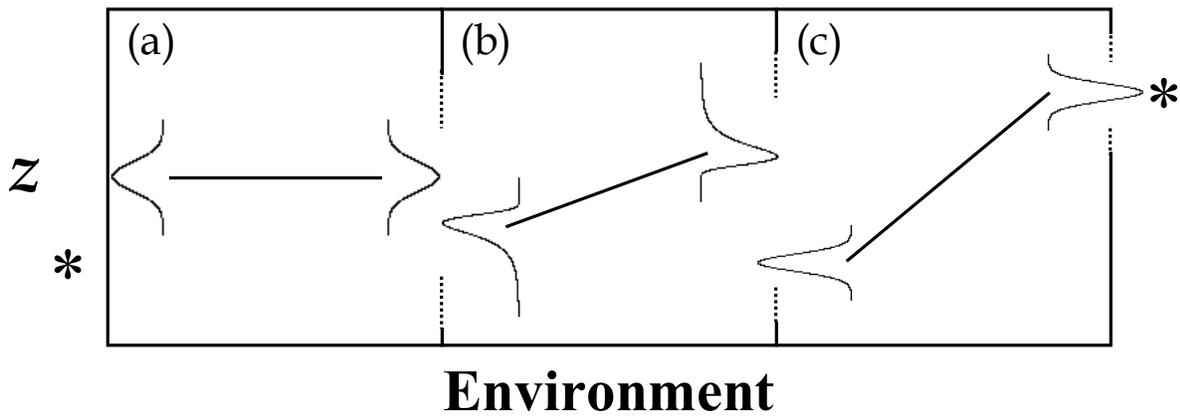
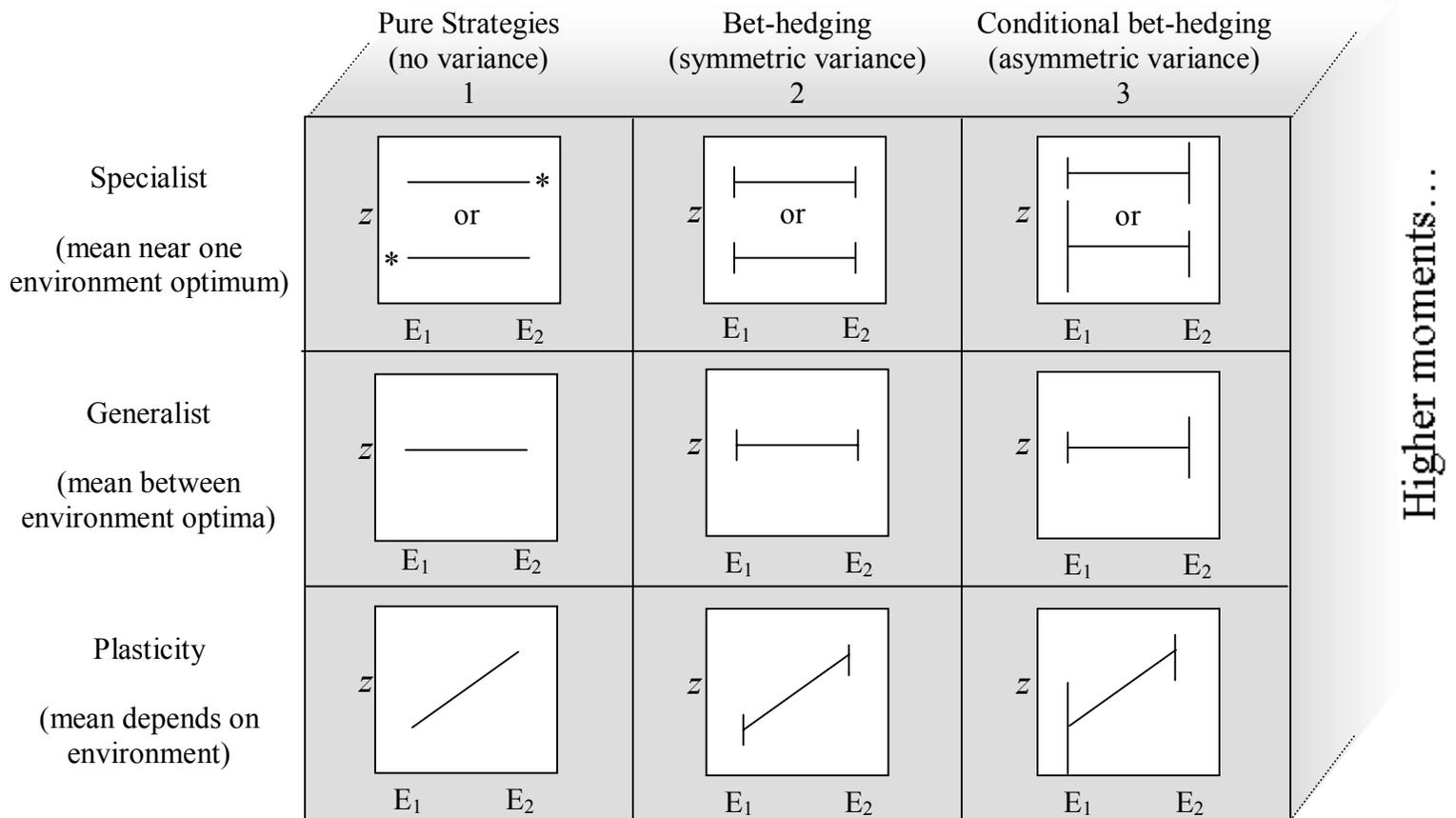


Figure 7.7. Evolution of multimoment reaction norms. Asterisks denote phenotypic optima in alternative environments and the progression of panels indicates the evolutionary trajectory. (a) A hypothetical population initially produces a flat reaction norm with phenotypes distributed normally in all environments. (b) Selection produces divergence in trait means and increases variances, skewness toward optima, and kurtoses (leptokurtosis). (c) When trait means reach phenotypic optima, selection produces symmetrical distributions with minimal variance. In the absence of constraints, the endpoint of evolution should be perfect plasticity (i.e. no variance within environments).



Box 7.1. Multimoment reaction norms, where z = trait values and E_i represent alternative environments. Column 1 illustrates the traditional “pure” strategies of specialization, generalization and phenotypic plasticity. Bet-hedging is depicted in Column 2, where variance is added to the former three strategies. (Note that the generalist strategy with added variance is the traditional “bet-hedger” in ecological modeling). Asymmetric bet-hedging, where variance differs by environment, is depicted in Column 3. That is, the amount of developmental noise might be conditional, perhaps based on the adaptive optimum level of variance prescribed by each environment.

In the two dimensions presented in this figure, we describe an expansion from the traditional suite of four strategies to nine. In theory the strategy space involves not only trait means and variances but all aspects of phenotype distributions. For example, a third dimension of this box could describe strategic flexibility in skewness, or kurtosis (see Discussion). The strategies shown here also can be extended to include nonlinear reaction norms across environmental gradients. Thus the most general framework for understanding phenotypic strategies is one of multimoment (polynomial) reaction norms.