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Developmental instability as a bet-hedging strategy

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In temporally varying environments selection will often act, at the expense of expected fitness in any given generation, so as to maximize geometric mean fitness across a number of generations (Gillespie 1977). Such "bet hedging" (Slatkin 1974) may occur in two ways (Seger and Brockmann 1987). In conservative bet hedging a genotype minimizes the risk of a very low fitness bout by producing a narrowly unimodal distribution of "safe" trait values. In contrast, a genotype practising diversification bet hedging spreads the risk by producing traits with increased variance (see Philippi and Seger 1989 for a full discussion). A classical example of such diversification both in theoretical and empirical studies is that of seed germination behaviour (Cohen 1966, Janzen 1977, Venable and Lawlor 1980, Cooper and Kaplan 1982, Bulmer 1984, Ellner 1985, León 1985, Venable 1985, Kalisz 1986, Bull 1987, Venable and Brown 1988, Biere 1991), but diversification or multiple strategies (Lloyd 1984) could be equally relevant to other processes such as insect diapause (Tuljapurkar and Istock 1993). Little is known, however, about how such within-genotype diversification might be produced. Here we propose that diversification bet hedging may be attained through a mechanism traditionally considered to be exclusively detrimental: developmental instability. We discuss the plausibility of this perspective, present testable hypotheses that emerge directly if bet hedging is achieved through instability of development, and suggest appropriate tests of these hypotheses. In this paper we discuss the mechanisms underlying diversification bet hedging although these mechanisms should apply to other, nonbet-hedging situations in which within-genotype trait variance is shown to be adaptive (see Geritz 1995 for density-dependent selection of seeds under spatial heterogeneity).

There exists considerable confusion surrounding the use of terms related to the degree of variability inherent to developmental processes (Zakharov 1992). The relative fidelity of development to a program is known variously as developmental stability (Mather 1953, Waddington 1957, Parsons 1992, Møller 1995), homeorhesis (Waddington 1957), homeostasis (Lerner 1954, Orzack 1985, Parsons 1992, Møller 1995), buffering capacity (Van Valen 1962), and developmental canalization (Mather 1953, Thoday 1958, Waddington 1960, Levin 1988). The mechanisms which these terms describe all have the effect of decreasing trait variance. Developmental instability, environmental sensitivity (Jinks and Pooni 1988), and phenotypic plasticity (Bradshaw 1965, Via and Lande 1985, Schlichting 1986) are all means by which trait variance is increased. There is considerable overlap in the definitions of some of these terms, and their usage may vary by author (Zakharov 1992).

Phenotypic variance expressed among individuals of a genotype is usually attributed to two general sources: plasticity and noise. Plasticity is measured as the phenotypic expression of genotypes across an environmental gradient, whereas developmental noise is assumed to result from random errors of development, but in fact is variance resulting from all sources unknown. Developmental noise, then, may include plasticity in response to environmental variables that have not been identified (Bradshaw 1965). There is ample evidence for the existence of genetic variation for plasticity (Bradshaw 1965, Perkins and Jinks 1971, Schlichting and Levin 1986, Scheiner et al. 1991, Oyama 1994). Although phenotypic plasticity is the variable expression of a genotype under differing environmental circumstances, it is quite possible to have well-canalized reaction norms, and the degree of plasticity is a genotype-level property. There is no reason to suppose that, like plasticity, developmental noise could not be maintained at some optimal level by stabilizing selection.

The genetic basis of developmental stability is not yet well established (see Clarke 1993 for a discussion of competing hypotheses). Developmental instability may be assessed through the occurrence of phenodeviants or, in (normally) bilaterally symmetrical organisms, as the fluctuating asymmetry (FA) of paired characters

(Mather 1953, Waddington 1957, Palmer and Strobeck 1986, Parsons 1992, Polak and Trivers 1994, Møller 1995), and trait stability has been found to have a genetic basis (Mather 1953, Thoday 1958, Waddington 1960, Kaufman et al. 1977, Scheiner et al. 1991). It is probable, however, that developmental noise would be much reduced under the homogeneous conditions typically used in breeding experiments; the fine-grained environmental variability of field conditions has the effect of increasing the environmental component of phenotypic variance of quantitative traits (Simons and Roff 1994). Fluctuating asymmetry is a weak indicator of developmental instability, and heritability estimates of FA are likely to severely underestimate the heritability of developmental instability (Whitlock 1996). Any among-genotype differences in the stability of phenotypic expression could be acted on by natural selection and, analogously to norms of reaction, the degree of instability would be considered a property of the genotype. It is apparent that trait variance in the case of plasticity is capable of adaptive evolution; the set of conditions under which fitness would be a function of developmental stability is less evident.

The prevailing view of developmental stability is one in which the production of variation is interpreted as an inferiority: the inability of a genotype to control the effects of the environment in the development of the phenotype. Møller's (1995) statement, "Fluctuating asymmetry (FA) is an epigenetic measure of the lack of developmental homeostasis and thus a measure of the inability of individuals to cope with genetic and environmental stress", and the assertion of Stearns et al. (1995) that "stabilizing selection should favor improved canalization, and the degree of a trait's canalization should be positively correlated with its impact on fitness" typify a conviction well-founded in results of recent research (Polak and Trivers 1994). It has been recognized, though, that by an indiscriminate acceptance of this interpretation of instability, other interpretations are ignored (Kaplan and Cooper 1984). Simply because it has been demonstrated that stress may lead to instability which, in turn, leads to asymmetry does not a priori imply that selection cannot favour instability. Circumstances under which selection favours high phenotypic variance have been described (Wourms 1972, Real 1980, Venable and Lawlor 1980, Crump 1981, Kaplan and Cooper 1984, Bull 1987, Geritz 1995), and we suggest that developmental instability may be maintained in a character by the direct action of selection or, indirectly, by selection on a correlated character. In some cases, then, fluctuating asymmetry might well be explained as a correlated response to selection for developmental instability in an associated trait.

In an unpredictable environment, elevated variance in traits closely related to fitness (such as hatching or germination timing) can lead to low temporal variance in fitness (Gillespie 1977). Instability would be interpreted as a bet-hedging strategy (Slatkin 1974, Philippi and Seger 1989) if it reduces the intergenerational variance in mean fitness of a genotype (thus increasing its long-term geometric mean fitness) by producing a diversity of phenotypes within a generation (Slatkin 1974; see Orzack 1985 for situations under which fitness homeostasis would not be expected to evolve). If the intergenerational environmental variance is high enough compared to the within-generation stabilizing selection on a trait such as germination time, a bet-hedging strategy is expected to evolve (Bull 1987).

Whereas the theoretical treatment of bet hedging has progressed rapidly, empirical validation of theory has been slower, perhaps impeded by difficulties related to the comparison of variances and by the practical difficulties associated with obtaining sample sizes large enough to estimate trait variances rather than simple trait values. A trait extensively cited as a possible bet-hedging trait, and the one used here as a model character for the purpose of discussion, is seed heteromorphism; a single genotype produces two or more seed types which behave differently under similar environmental conditions. The mechanism whereby a single genotype may produce seeds which differ in their germination behaviours is not well understood, and possibilities presented in the literature include individual genetic bases for seeds at different positions (in the case of seed dimorphism), differential timing of seed development and thus stage of maturation of seeds within plants (Silvertown 1984), change in developmental constraints within plants through time (Wolfe 1995), and the resource status or size of individual plants (Venable 1992, Philippi 1993). Developmental instability could also explain diversified germination behaviour of seeds produced by a single genotype, and would be selected for to the extent to which bet hedging was appropriate.

Considering annual plant species with seed banks, Cohen (1966) modelled germination under various regimes of temporal uncertainty, and found that selection should favour a lower germination fraction per generation when the probability of success was less predictable. In addition to germination variance associated with seed banks, developmental instability is equally relevant to variance in germination timing within a season or generation under coarse-grained environmental uncertainty, the type modelled by León (1985) and Venable (1989), and discussed by Silvertown (1985) and Marks and Prince (1981). Size and germination are largely controlled by the parent plant, and germination strategies should evolve to maximize parental fitness (Westoby 1981, Silvertown 1984). Marks and Prince (1981) showed that for *Lactuca serriola*, plants produced by seeds that germinate later in a season suffer a fecundity cost in relation to early germinators, but these plants may act as insurance against the complete loss of the early cohort character-

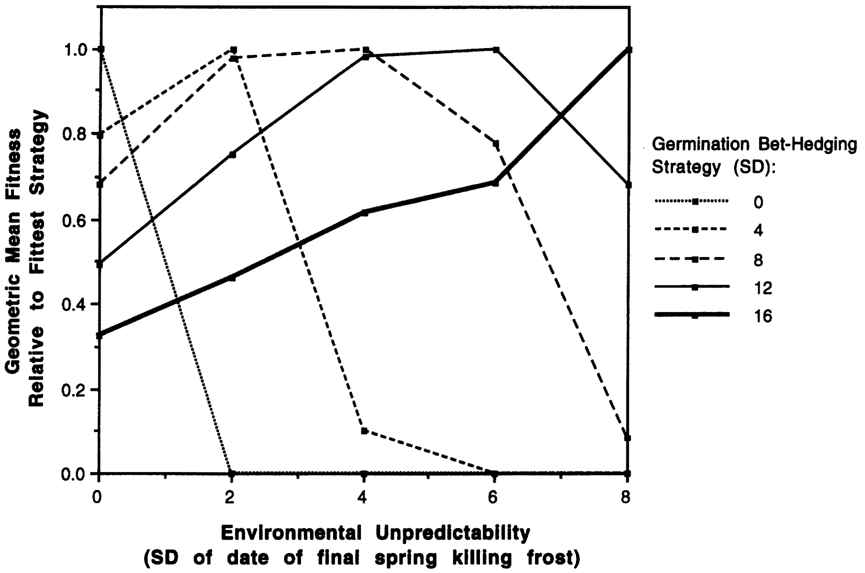

Fig. 1. Results of a model comparing long-term fitness of five germination strategies differing in within-season diversification, under five levels of environmental unpredictability. This model shows that the level of unpredictability characterizing the environment determines which of the bet-hedging strategies has the highest relative geometric mean fitness: the optimum germination variance increases with increasing unpredictability of final spring frost, and only in the case of zero unpredictability is synchronized germination selected for. The length of any particular growing season was randomly assigned from a normal distribution with a mean of 100 d and standard deviation given by the level of unpredictability. The mean germination date was fixed, regardless of diversification strategy, and was equal to the mean date of final spring frost. The germination date of an individual seed was drawn randomly from a normal distribution with a standard deviation given by the diversification strategy of its parent. Seeds germinating before the final frost at the beginning of the season did not survive, and were assigned a fitness of zero; seeds germinating after the final frost survived, but the fitness of late germinators was discounted in proportion to the relative time "wasted" by not germinating immediately after the final frost. The geometric mean fitness was calculated over thirty seasons, and each of the 25 fitness estimates represents the average from twenty runs of the simulation program. Fitnesses were scaled to a maximum of one for each level of environmental unpredictability.

ized by high mortality. In the cricket *Gryllus pennsylvanicus*, delayed hatching has the same result; late hatchers develop quickly and become small adults (Carrière et al. 1996). Within-season diversification, then, analogously to among-season germination diversification through the production of a seed bank, promotes the avoidance of unpredictable bouts of detrimental conditions within a season for at least some of the seeds produced by an individual: a plant producing seeds that germinate simultaneously has a high fitness if the time happens to be "right" (no killing frost occurs after germination, for example) relative to a plant whose seeds germinate less synchronously. If the timing is "wrong", though, the synchronous genotype's relative fitness could be close to zero. The mathematics describing within-season diversification in bet hedging are very involved (León 1985), and have rarely been attempted. Here we present results of a model simulating the fitness consequences of seed germination diversification strategies within a season (Fig. 1). Because natural selection acts on geometric-mean fitness, the cost of a season of low fitness is higher than the benefit of a correspondingly good season, and platykurtic distributions of seed germination time are expected to evolve in response to unpredictable environments. Therefore, under environmental unpredictability, individuals producing seeds whose germination timing is highly unstable and thus more variable would be at a selective advantage.

Predictions and tests

Under the traditional interpretation, directional selection acts to minimize developmental instability, especially in fitness characters (Stearns et al. 1995). When a particular level of instability benefits a genotype through an increase in its geometric mean fitness, stabilizing selection acts on developmental instability. If a bet-hedging strategy can be attained through developmental instability by an increase in the variance in seed germination behaviour, and if this instability is expressed pleiotropically in another trait such as cotyledon asymmetry, then a correlation between these two traits is produced. Four main predictions follow directly in cases where instability of a bet-hedging trait can be observed as fluctuating asymmetry. First, when additive genetic variation exists for the variable expression of a bet-hedging trait within a population, genotypes exhibiting high variance will also show high FA of an associated bilateral trait. Second, populations expressing comparatively high diversification in a bet-hedging trait will also show high FA in that or a developmentally related trait compared to a population expressing relatively low diversification. The third prediction arising from the hypothesis that bet hedging may be generated by developmental instability is that populations inhabiting relatively unpredictable environments should show both high diversification (germination variance, for example) and FA. Fourth, because bet hedging is predicted to be more prevalent in short-lived than long-lived species (Seger and Brockmann 1987: 195), annual species are expected to show higher FA in traits related to bet hedging than are either biennials or perennials.

Tests of the above predictions demand that a bet-hedging trait be identified, and that a second, developmentally related trait, be available for the direct measurement of instability. It should be highlighted here that such an observation would not be indicative of the presence of bet hedging; such an inference would require a study of the fitness consequences of the generation of trait variance. Given the efficacy of the trait to act as a bet-hedging strategy, though, selection for developmental instability would be a possible mechanism underlying the evolution of diversification.

Experiments intended expressly for the purpose of testing the association between bet-hedging traits and instability should be designed to identify this association within genotypes, and should exclude the conflation of unintended causes of this association. To test the within-population, among-genotype association of germination variance and cotyledon asymmetry, for example, an appropriate design would partition the among-seed, within-genotype variance from other sources including block effects and maternal effects. The design would be much simplified by using a completely self-fertilizing species because genetic identity among seeds of a single parent may be assumed. Partitioning of these effects could be achieved by first growing several parental plants of each genotype at randomized positions within blocks in a controlled environment. With the seed produced by these parental plants, a number of germination blocks (Petri dishes, for example) could be established, and one seed from every parental plant of every genotype randomly allocated to a position within each block. Replication, in a design where observations consist of a measure of variance, may be accomplished by including sufficient numbers of blocks so that each block may be preassigned to one of two (for example) replicate treatments. As an alternative to replication, bootstrapping techniques could be used to obtain sample variances of the coefficients of variation of germination time for each genotype. Subsequent analysis on measurements of time to germination and cotyledon FA could then attribute the covariance of these two traits to its genetic, maternal, and environmental sources.

A selection experiment could also be designed to test the association between developmental instability and a potential bet-hedging trait. Again using the example of cotyledon asymmetry and CV of germination time; high asymmetry, low asymmetry, and control lines could be established and one could determine the correlated response in the variability of germination time.

The viability of these predictions and tests rests on four assumptions. First, that the observed variance is an effective bet-hedging trait. Because a bet-hedging trait is one which maximizes the long-term geometric mean fitness, theoretical support for the existence of such traits is far more advanced than is empirical support. A second assumption is that developmental instability can produce a diversification of phenotypic expression in the bet-hedging trait. A further complication may arise if other causes of diversification behaviour obscure the diversification generated by instability. Third, it is necessary that developmental instability producing the diversification can be independently assessed by a known index of instability such as FA. Cases in which the diversification trait is itself amenable to FA measurement would not be as difficult as ones in which the diversification trait is more remotely associated with the trait amenable to FA measurement. The presence of strong genetic correlations among the means of traits does not imply that FA will be correlated. There is little empirical support for among-trait correlations of fluctuating asymmetry (Palmer and Strobeck 1986) but, because the aim of these studies was usually to compare instability of different kinds of traits or to test whether instability is an organism-wide phenomenon, the traits chosen may have been more developmentally distinct than traits most useful for testing the association between instability and bet hedging. Because FA is only a weak indicator of instability, even when strong among-trait genetic correlations for developmental instability exist, the expected correlations involving FA are much lower (Whitlock 1996). Clearly, investigations of genetic correlations of instability among traits are needed.

Finally, the predictions and tests, as well as the proposition itself that developmental instability is a possible bet-hedging mechanism, rest on the assumption that variation in developmental instability is explained partially by additive genetic variation. In a recent meta-analysis, Møller and Thornhill (1997) concluded that FA has a relatively low (0.27) but significant heritability. Far from closing the issue of FA heritability, this meta-analysis provoked several harsh solicited commentaries disclaiming the validity of its findings (Markow and Clarke 1997, Palmer and Strobeck 1997). The one point on which there seemed to be agreement, though, is that there is a lack of heritability analyses in the literature. Negative results in a test for the association between developmental instability and trait diversification could imply either that instability is not a bet-hedging strategy, or that one or more of the above assumptions do not hold.

Summary

Developmental instability and bet hedging have been regarded as disparate fields of study. Diversification bet-hedging strategies are said to have evolved if a genotype's intergenerational fitness is increased, to the detriment of short-term expected fitness, by risk spreading. A trait of low developmental stability is more sensitive to the effects of the environment than is a trait of higher developmental stability, and thus exhibits more developmental "noise". This noise would be advantageous if it has the effect of increasing the phenotypic variance of a bet-hedging trait.

We argue that, given the appropriateness of variance (in timing of germination, for example) as a bet-hedging strategy, developmental instability is a possible and unappreciated mechanism by which it evolves. The extensive interpretation of fluctuating asymmetry as the "inability" of a genotype to direct its development is appropriate given the results of much recent research. Such interpretations should be made with caution if the asymmetrical character is closely associated with another that may exhibit instability as a bet-hedging strategy. Studies specifically designed to assess the genetic basis of instability in characters such as seed germination behaviour would greatly enhance our understanding of the potential for the evolution instability as a bet-hedging strategy: developmental instability may not only be the inability to stabilize, but the ability to destabilize development.

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