

## EVOLUTION OF PHENOTYPIC VARIANCE

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*Abstract.*—A cornerstone of evolutionary theory is that the phenotypic variance of a population may be partitioned into genetic and environmental (nonheritable) components. The traditional motivation for this distinction is that the rate of evolution under natural selection depends on the (relative) magnitudes of certain genetic components of variance. The components of variation are also interesting from another perspective, as illustrated here. Phenotypic variation may be selectively maintained in a population according to its components: selection may favor the maintenance of only the environmental components, only the genetic components, or be indifferent to the composition of the variance. Even when selection is shown to favor phenotypic variation regardless of its components, the possibility exists that environmental variance will evolve to displace the genetic components or vice versa. Environmental and genetic factors may thus compete to produce a given selected level of phenotypic variance. A test of some of these models is provided from the example of seed dormancy: the prediction that variation in seed germination time should be purely environmental is supported by the demonstration of low heritability of germination time in the two available studies.

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Two types of factors are recognized as contributing to the phenotypic variation in a population, genetic and environmental. For example, adults of the same age may differ in body size because they experienced different levels of nutrition as juveniles (an environmental factor) or because they inherited differences in the propensity for growth (genetic factors). Genetic factors are critical to evolutionary change under natural selection, and the maintenance of genetic variation has been a central issue of evolutionary biology since Darwin. Although a common effect of natural selection is to ultimately erode genetic variation, special cases are known in which natural selection actively preserves genetic variation (as shown chiefly with population genetic models; Crow and Kimura, 1970 pp. 236-238, 256-258). In a similar vein, various models have identified conditions in which natural selection favors the maintenance of environmental variance or phenotypic variance of unspecified components (e.g., Cohen, 1967; Horn, 1969; Slatkin and Lande, 1976; Slatkin, 1978; Real, 1980; Caswell, 1983; Bulmer, 1984; Kaplan and Cooper, 1984; Ellner, 1985*a*, 1985*b*; León, 1985; Via and Lande, 1985).

Whenever selection is found to maintain phenotypic or genetic variation, a further question may be considered as to whether selection maintains genetic factors on an equal basis with environmental factors. A

given magnitude of phenotypic variation can be generated purely from environmental effects, purely from genetic effects, or from any intermediate combination, and selection may be indifferent to the combination or may maintain only one component. Although the environmental component of a phenotype is itself not heritable, the susceptibility of an individual to environmental effects is a property that often has a genetic basis (as with temperature-sensitive mutations) and thus can evolve under natural selection.

This paper will demonstrate that the selected maintenance of genetic variation does not imply the maintenance of environmental variation, and conversely, that the selected maintenance of environmental variation does not imply the maintenance of genetic variation. This conclusion has been reached in some previous studies of specific biological problems, and a major objective here is to bring these diverse examples into one perspective. To illustrate the wealth of possible applications of this perspective, population genetic models representing a variety of biological settings will be presented. Specifically, model 1 will represent frequency-independent density-independent selection of a continuous trait, model 2 will address frequency-independent density-independent selection of a discrete trait, and model 3 will treat frequency-dependent selection of a discrete trait. All cases will be

analyzed under temporally constant selection as well as under fluctuating selection. The models will be restricted to the evolution of traits whose expression within an individual is fixed during the relevant part of its life history; the present framework may be extended to traits whose expression varies over the life of an individual (such as behaviors), but such considerations are beyond the scope of this study. The Discussion will offer an empirical test of one of the models.

*Phenotypic Plasticity Versus Random Environmental Variation.*—A nongenetic component of phenotypic variation may be classified as random or systematic (Falconer [1981] used the terms "special" and "general"). Random environmental variation, or developmental "noise," is used to describe variation that is uncorrelated with external cues. An alternative form of environmental variation is phenotypic plasticity, in which the phenotype varies systematically with some environmental cue; the "norm of reaction" describes the phenotype produced under different environmental conditions. For example, in considering the duration of diapause in a genetically homogeneous strain of insects, the duration might vary among individuals reared under apparently identical conditions, due to random effects, and the duration might also decrease with increasing ambient temperature, indicating phenotypic plasticity. The models in this paper contrast genetic factors with random environmental factors as alternative bases of phenotypic variance; they do not address phenotypic plasticity (see Via and Lande, 1985; Lloyd, 1984, for analyses of phenotypic plasticity).

*Frequency-Independent,  
Density-Independent Selection*

*Model 1: Continuous Characters.*—This section analyzes a model of stabilizing selection on a continuous character with an optimum that varies between generations, as in the study of Slatkin and Lande (1976). As biological motivation for the model, imagine an insect with the following life history. Eggs are laid in late summer, larvae hatch in spring and feed throughout much of summer prior to pupation. Eclosion yields

adults that reproduce and die in late summer (discrete, nonoverlapping generations).

The model to be presented will investigate evolution of a characteristic such as the time of pupation (or its logarithm), represented by the variable  $x$  which potentially ranges over the entire real axis. The time of pupation is subjected to stabilizing selection, as in the case that early pupators yield small adults, and late pupators face a deteriorating environment for egg deposition. Climatic variation causes the optimum time of pupation to vary between years.

The model is parameterized as follows. An individual's fitness as a function of its value of  $x$  in generation  $t$  is Gaussian,

$$s(x, \psi_t) = ce^{-\frac{(x-\psi_t)^2}{2\omega^2}}, \quad (1)$$

where  $\psi_t$  is the optimum,  $\omega^2$  determines the strength of selection toward  $\psi_t$ , being more extreme with smaller values, and  $c$  is a suitably chosen positive constant (whose value will be irrelevant to the final results). Fitness is therefore independent of population density and of the frequency of individuals with different values of  $x$ .

Each genotype is subject to variation in the value of  $x$  that it develops. The distribution of  $x$  within genotype  $k$ ,  $\phi(x|k)$ , is normal with mean  $\mu(k)$  and variance  $\sigma_e^2(k)$ , both constant in time but possibly varying between genotypes. The within-genotype variation,  $\sigma_e^2(k)$ , is necessarily due to environmental factors, and it is further assumed that these environmental factors are uncorrelated with  $\psi_t$ . The total variance of  $x$  within the population is, for the general case of  $n$  genotypes and infinite population size,

$$\sum_{k=1}^n p_k \sigma_e^2(k) + \sum_{k=1}^n p_k [\bar{\mu} - \mu(k)]^2, \quad (2)$$

$$\bar{\mu} = \sum_{k=1}^n p_k \mu(k),$$

where  $p_k$  is the frequency of genotype  $k$ . The first summation represents the average environmental variance in  $x$ , and the second term is the variance in means. Note that  $\sigma_e^2(k)$  and  $\mu(k)$  may vary independently among genotypes.

The fitness of a genotype  $k$  over the period of selection within one generation is

$$w(k, \psi_t) = \int_{-\infty}^{\infty} \phi(x|k)s(x, \psi_t) dx$$

$$= \frac{ce^{-\frac{[\mu(k)-\psi_t]^2}{2[\sigma_e^2(k)+\omega^2]}}}{\sqrt{\sigma_e^2(k) + \omega^2}} \quad (3)$$

In the absence of temporal fluctuations ( $\psi_t = \bar{\psi}$  for all  $t$ ), each genotype's fitness is constant through time. Differentiation of (3) with respect to  $\mu(k)$  and  $\sigma_e^2(k)$  reveals that a genotype achieves the maximum possible fitness with  $\hat{\mu} = \bar{\psi}$  and  $\hat{\sigma}_e^2 = 0$  (the circumflex designating optimal values of the mean and variance, respectively, which do not depend on genotype). Thus both genetic and environmental components of phenotypic variation are selected against in a temporally constant environment provided that a homozygote can obtain these optimal values.

Incorporation of temporal variation in  $\psi_t$  can select environmental variance but does not, by itself, select genetic variance. With  $\psi_t$  as a random variable, distributed independently and identically for different  $t$  (with mean  $\bar{\psi}$  and variance  $\pi^2$ ), this problem may be analyzed with methods derived for stochastic selection (Gillespie, 1973; Karlin and Liberman, 1974, 1975). Let genetic variation in  $x$  occur at one locus with two alleles, allele  $A$  rare and  $a$  common, such that selection of  $A$  can be approximated by ignoring "second-order" terms (e.g., by ignoring  $AA$  individuals). A population consisting mostly of  $aa$  individuals is stochastically stable to invasion by  $A$  if

$$E\{\ln[w(aa, \psi_t)]\} > E\{\ln[w(Aa, \psi_t)]\}, \quad (4)$$

where the expectation is taken over  $\psi_t$ . (Karlin and Liberman [1975] indicated that this result holds even for autocorrelated  $\psi_t$ , provided that  $\psi_t$  and  $\psi_{t+k}$  are asymptotically uncorrelated as  $k \rightarrow \infty$ .) Thus, if  $E\{\ln[w(k, \psi_t)]\}$  is maximized over  $\mu(k)$  and  $\sigma_e^2(k)$ , a common homozygous genotype adopting those parameter values is stochastically stable to invasion by alternative alleles; hence these values constitute an evolutionarily stable strategy.

From (3),

$$E\{\ln[w(k, \psi_t)]\} = \ln(c) - \frac{\ln[\sigma_e^2(k) + \omega^2]}{2}$$

$$- \frac{[\mu(k) - \bar{\psi}]^2 + \pi^2}{2[\sigma_e^2(k) + \omega^2]}$$

Maximization over  $\mu(k)$  yields

$$\hat{\mu} = \bar{\psi}, \quad (5a)$$

and maximization over  $\sigma_e^2(k)$  separately yields

$$\hat{\sigma}_e^2 = \begin{cases} \pi^2 + [\mu(k) - \bar{\psi}]^2 - \omega^2 & \text{if } \pi^2 + [\mu(k) - \bar{\psi}]^2 > \omega^2 \\ 0 & \text{if } \pi^2 + [\mu(k) - \bar{\psi}]^2 \leq \omega^2. \end{cases} \quad (5b)$$

If  $\mu(k)$  and  $\sigma_e^2(k)$  are maximized jointly, the term  $[\mu(k) - \bar{\psi}]^2$  in (5b) becomes zero:

$$\hat{\sigma}_e^2 = \pi^2 - \omega^2. \quad (5c)$$

Note that result (5) is exact and depends only on the mean and variance of  $\psi_t$ , not on the entire distribution. An extension of result (5) is derived for multiple, correlated characters (Appendix I), but the main conclusions are evident from the single-character case.

Result (5) embodies several conclusions of biological interest. First, environmental variance in  $x$  is favored if the magnitude of fluctuation in the optimum ( $\pi^2$ ) is sufficiently large relative to the magnitude of stabilizing selection on the character ( $\omega^2$ ). As the temporal variance in the phenotypic optimum increases, so does the advantage for a genotype in producing a range of phenotypes, so that some individuals with that genotype are assured of developing a value of  $x$  near the optimum each generation. A threshold for positive selection of environmental variance is observed such that minor variation in the optimum entails selection for zero environmental variance. However, the condition  $\pi^2 > \omega^2$  can be achieved with an infrequent but harsh environment.

A second conclusion is that genetic variance is not encouraged by fluctuating selection. If one regards the evolution of rare alleles differing only in  $\mu(k)$  as a limiting case for the evolution of genetic variance, the result that a genotype producing  $\mu(k) = \bar{\psi}$  cannot be invaded indicates that genetic

variance is always reduced by selection in this model [holding  $\sigma_e^2(k)$  constant]. This finding parallels Lande's (1977) demonstration that, in the absence of mutation, the additive genetic variance of a polygenic character is ultimately eliminated under Gaussian selection, regardless of whether the optimum varies between generations. However, the maintenance of genetic variance is not precluded by result (5) and depends on the genetic constraints of the population. For example, if only a heterozygote can achieve the optimal value, genetic variance will be maintained from the unavoidable production of homozygotes even though their values of  $\mu(k)$  and  $\sigma_e^2(k)$  are suboptimal. Such qualifications about genetic constraints often apply to analyses of evolutionarily stable strategies (Maynard Smith, 1982 pp. 40–47).

Slatkin and Lande (1976) investigated selection of phenotypic variance in a polygenic character, and their results warrant comparison with those here. Their model differed from model 1 in two important respects. First, their character was assumed to be composed of additive genetic and environmental variance with heritability  $h^2$ ; second, their rare modifier of environmental variance also affected the additive genetic variance in such a way that the heritability was not changed. As in model 1, their fitness function was Gaussian with a time-varying optimum.

Slatkin and Lande observed that a rare allele increasing the environmental variance was favored if  $\pi^2 > \omega^2/(1 + h^2)$ ; conditions were not derived for an equilibrium level of variance. The present result (5) is similar to their result except for their inclusion of  $h^2$  (which is assumed to be 0 at equilibrium in model 1). Since  $h^2$  influences their selection threshold, it is reasonable to anticipate that the evolutionarily stable level of environmental variance would also be modified. However, my numerical study of fluctuating selection on a quantitative character with multiple loci did not support this suggestion; rather result (5c) seemed to be supported (Appendix II).

*Model 2: Discrete Characters.*—A model of frequency-independent selection on a discrete character yields the same qualitative conclusion as did the previous model

of a continuous character: genetic and environmental variance are each disfavored under temporally constant selection, but environmental variance is sometimes favored under fluctuating selection. The model of discrete variation can be introduced in the biological context of seed germination in an annual plant. The hypothetical population consists of an infinite number of hermaphrodites. Seeds are produced in summer and germinate either in fall or the following spring, so only two discrete phenotypes are recognized. Fall germination may lead to death during winter, but plants that survive winter have much higher fecundity than spring-germinated plants. Reproduction occurs in summer regardless of the individual's germination date, and adults die.

The model offered here investigates the evolution of environmental and genetic variation in the time of germination. The present analysis is similar in some ways to the analyses of Cohen (1966, 1967), Bulmer (1984), Ellner (1985a, 1985b) and León (1985). Their models of discrete characters considered the alternative phenotypes of germination versus dormancy within a generation, so that one phenotype consisted of the failure to breed during the current generation, with the possibility of future germination and reproduction. Although biologically different, the two problems can be parameterized identically in models that do not consider population density. Except for Bulmer, those authors did not address the evolution of environmental versus genetic variance in germination time, but many of the algebraic results required below were derived in their studies. Furthermore, and as noted by León (1985), although Cohen's results were described in terms of maximizing population fitness, the frequency-independent nature of selection renders many of his analyses appropriate for some types of genetic models.

Let  $z(k)$  be the probability that seeds of genotype  $k$  germinate in fall; let  $1 - z(k)$  be the probability of germination in spring. In generation  $t$  fall germinators have expected fitness of  $w_t$  relative to the fitness of spring germinators. To facilitate presentation and analysis of the model, most of the life cycle will be treated as haploid. Diploidy lasts only a brief period following conception,

then one allele is eliminated at random from each locus, creating a permanent haploid (while still a seed). In a population with  $n$  alleles,  $A_1, \dots, A_n$ , representing  $p_k$  as the frequency of  $A_k$  in haploid seeds, and assigning a phenotypic value of unity to fall germination and zero to spring germination, the total phenotypic variance may be partitioned as

$$\begin{aligned} \bar{z}(1 - \bar{z}) &= \sum_{k=1}^n p_k z(k) [1 - z(k)] \\ &+ \sum_{k=1}^n p_k [\bar{z} - z(k)]^2, \\ \bar{z} &= \sum_{k=1}^n p_k z(k), \end{aligned} \quad (6)$$

as in (2), with the first sum representing the environmental variance and the latter sum the genetic variance. The value of  $\bar{z}$  represents both the mean of this binary character and the average probability of fall germination in the population. Note that because of the binary property of the character, the values of  $z(k)$  determine both the mean and variance, so that means and variances are not independent among genotypes, unlike in model 1 of the continuous character.

The frequency of allele  $A_k$  in one generation as a function of its frequency in the previous generation is given by

$$\begin{aligned} p_k' &= \frac{p_k [z(k)w_t + 1 - z(k)]}{W}, \\ W &= 1 + (w_t - 1)\bar{z}, \end{aligned} \quad (7a)$$

where  $\bar{z}$  was given in (6). In a temporally constant environment such that  $w_t = \bar{w} = 1 + \delta$  for all  $t$ , (7a) can be rearranged as

$$\Delta p_k = \delta \frac{p_k}{W} [z(k) - \bar{z}]. \quad (7b)$$

As is well known, equilibrium is achieved only at the boundaries  $p_k = 0, 1$  or in the neutral cases of  $z(k) = z(j)$  for all  $k$  and  $j$ , or  $\delta = 0$  (no realized fitness difference between alleles). If  $\delta > 0$ , selection favors complete fall germination ( $\hat{z} = 1$ ), whereas if  $\delta < 0$ , selection favors complete spring germination ( $\hat{z} = 0$ ), subject to the limitations of available genetic variation. Genetic variation is never maintained, except in the

neutral cases noted above; since the individuals being selected are haploid, there is no counterpart to the diploid case of the maintenance of genetic variation through heterozygote superiority (which, in any case, is not the focus of this study).

This model is readily extended to incorporate fluctuating selection, and the following analysis in fact applies to a diploid as well as the haploid model. From (4), the stochastic stability of a common allele ( $A_1$ ), to invasion by a rare allele ( $A_2$ ) requires,

$$\begin{aligned} E\{\ln[w_t z(1) + 1 - z(1)]\} \\ > E\{\ln[w_t z(2) + 1 - z(2)]\}, \end{aligned} \quad (8a)$$

where the expectation is taken with respect to the random variable  $w_t$ . Due to the haploid inheritance in this model, conditions for invasion by rare  $A_2$  with  $A_1$  common are the reverse of conditions for invasion by rare  $A_1$  with  $A_2$  common, and genetic variation is not selected (Dempster, 1955; although Chesson, 1985, noted that fluctuating selection can maintain genetic variation in haploids with overlapping generations). Selection favors alleles with the highest value of  $E[\ln(w_t z + 1 - z)]$ , and the level of  $z$  that cannot be invaded is found as

$$\max_z \{E[\ln(w_t z + 1 - z)]\}. \quad (8b)$$

Consideration of (8b) at the boundaries  $z = 0, 1$  leads directly to Cohen's conditions for the maintenance of polymorphism:

$$E(w_t) > 1, \quad E\left(\frac{1}{w_t}\right) > 1 \quad (9)$$

(Cohen, 1966, 1967). Thus the arithmetic mean relative fitness of each phenotype must exceed unity. Although an exact solution to (8b) is not apparent for the general case, the second derivative of the term in braces in (8b) is strictly negative, hence (9) guarantees a unique, internal solution (León, 1985; some special cases were solved by León). Thus, as in model 1, either the absence of phenotypic variance is favored, or under certain types of fluctuating selection, pure environmental variance is favored.

This model has been extended in recent papers by Bulmer (1984), Ellner (1985a, 1985b), and León (1985), to include density-dependent and frequency-dependent selection (see also Discussion, below). Bul-

mer explicitly noted that both density-independent and density-dependent selection favored environmental variance in germination time. Model 2 is offered here, despite its similarity to Bulmer's analysis, to supplement the continuous-character model 1, to motivate empirical tests of this particular model, and to facilitate presentation of the frequency-dependent model (next).

#### *Frequency-Dependent Selection*

As an alternative to the models of frequency-independent selection, this section presents a model of frequency-dependent selection, whereby phenotypic variance is favored under temporally constant selection. The problem to be studied is whether a genetic basis of phenotypic variation is maintained differently than an environmental basis under constant as well as fluctuating selection.

*Model 3: Discrete Characters.* — The model here is largely the same as model 2 above (two phenotypes) and may be envisioned in the context of fall versus spring germination of seeds; the model is easily considered in other biological contexts as well. The major difference between this model and model 2 is that the relative fitness of phenotype 1 (fall germination) decreases as a larger proportion of the population adopts phenotype 1, and conversely for the fitness of phenotype 2. This model will also be developed to include temporal variation in the frequency dependence. Therefore, let  $w_t(\bar{z})$  represent the relative fitness of phenotype 1 in the population in generation  $t$ , where  $\bar{z}$  is the proportion of the population adopting phenotype 1, from (6). The functions  $w_t(\bar{z})$  are assumed to be monotonically decreasing over  $0 < \bar{z} < 1$ , and  $z_t^*$  is the point for which the two phenotypes are equally fit:  $w_t(z_t^*) = 1$ , with  $0 < z_t^* < 1$ .

*Constant selection.* — In this model, constant selection implies that the form of frequency-dependent selection  $w_t(\bar{z})$  remains the same between generations. For convenience of notation in this paragraph, designate  $z_t^*$  simply as  $z^*$ , and  $w_t(\bar{z})$  as  $w(\bar{z})$  since they do not depend on  $t$  under constant selection. With two alleles ( $A_1$  and  $A_2$ ), the population phenotypic equilibrium of  $\bar{z} = z^*$  is attainable only if  $z(1) \geq z^* \geq z(2)$  or  $z(1) \leq z^* \leq z(2)$ . For any two such al-

leles there is a unique equilibrium frequency of  $A_1$ ,  $\hat{p}_1$ , which is found as the solution to  $\hat{p}_1 z(1) + [1 - \hat{p}_1]z(2) = z^*$ . From (7b) with two alleles, gene frequencies always converge toward this equilibrium, but undamped oscillations in gene frequency may occur with certain types of fitness functions; local stability against undamped oscillations is guaranteed conservatively by  $w'(\bar{z})|_{\bar{z}=z^*} > -8$ . With three or more alleles differing in their  $z(k)$  values, a continuum of equilibria may exist. In particular, if  $z(1) = 0$ ,  $z(2) = 1$ , and  $z(3) = z^*$ , a continuum of equilibria exists from the one extreme of pure genetic variance ( $\hat{p}_3 = 0$ ,  $\hat{p}_2 = z^*$ ) to the other extreme of pure environmental variance ( $\hat{p}_3 = 1$ ), and evolution is indifferent to the relative combination of environmental and genetic components of variance. Such equivalence of genetic and environmental variance at the polymorphic equilibrium has been recognized in several previous models of frequency-dependent selection (e.g., Maynard Smith, 1982; Slatkin, 1978; Bulmer, 1984).

*Fluctuating selection.* — The evolutionary process under frequency-dependent selection is no longer indifferent to the relative contribution of genetic and environmental variance when selection fluctuates between generations. Again it seems that temporally variable selection favors environmental variation over genetic variation, but this effect is weaker than in the preceding models.

Fluctuating selection was studied by numerical methods for a restricted set of fitness functions in the context of model 3:  $w_t(\bar{z}) = a_t - b_t \bar{z}$ ,  $= \exp(a_t - b_t \bar{z})$ ,  $= a_t - b_t \sin[\pi(\bar{z}/2)]$ , with  $a_t$  and  $b_t$  chosen positive so that  $w_t(\bar{z})|_{\bar{z}=0} > 1$  and  $0 < w_t(\bar{z})|_{\bar{z}=1} < 1$ . The latter two fitness functions are convenient examples of nonlinear functions. Three alleles were assumed,  $z(1) = 0$ ,  $z(2) = 1$ ,  $0 < z(3) < 1$ . When one or both of the parameters  $a_t$  and  $b_t$  were varied between generations, independently of each other and independently of previous generations, selection invariably favored environmental variance over genetic variance (Fig. 1). Thus, an allele  $A_3$  coding for  $z(3) = E(z_t^*)$  drove  $A_1$  and  $A_2$  toward low frequencies, as if to extinguish them. Similarly, with  $z(3) > z^*$  [ $z(3) < z^*$ ], allele  $A_3$  drove  $A_2$  ( $A_1$ ) toward extinction but the other allele was maintained.

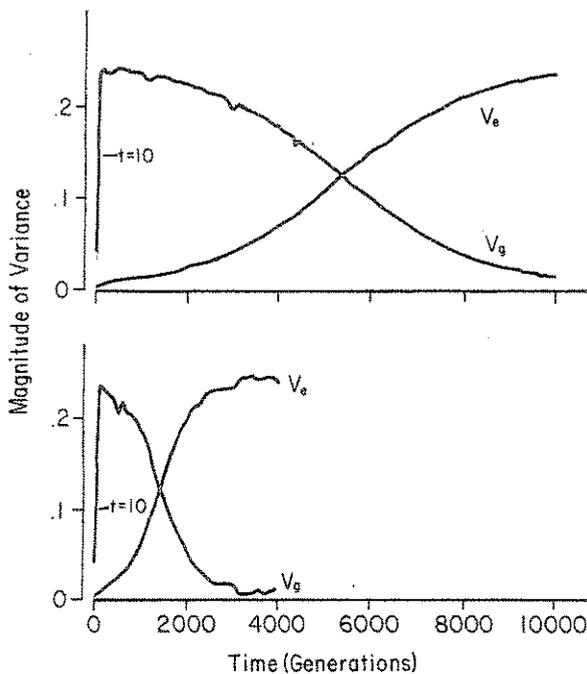


FIG. 1. Evolution of genetic and environmental variance under fluctuating, frequency-dependent selection. Text model 3 with two phenotypes was studied numerically for three alleles,  $A_1$ ,  $A_2$ , and  $A_3$ , each with different probabilities of exhibiting phenotype 1: 0, 1, and 0.5, respectively. Top and bottom graphs represent different trials. Under temporal variation in the frequency-dependent fitness functions, two phases of evolution are observed. First, rapid quasi-equilibration of the phenotypic variance occurs, largely through changes in the genetic variance (the curve indicated by  $V_g$ ); the arrow at  $t = 10$  indicates the genetic variance at generation 10. Second, the genetic variance is gradually displaced by environmental variance ( $V_e$ ), keeping the total phenotypic variance ( $V_g + V_e$ ) relatively constant. Environmental variance evolves more rapidly as the temporal variance in fitness is increased (compare top and bottom graphs). The function of frequency-dependent fitness used in these simulations was  $w_t(\bar{z}) = 1.2 - (0.4 + \delta)\bar{z}$ , where  $\delta$  was chosen each generation from a uniform distribution with a mean of zero, independently of previous generations, and  $\bar{z}$  was the frequency of phenotype 1 in generation  $t$ . The variance of  $\delta$  was 0.02 in the top graph and 0.08 in the bottom graph. In both trials, starting frequencies of alleles  $A_1$ ,  $A_2$ , and  $A_3$  were 0.04, 0.95, and 0.01, respectively. Environmental and genetic variances were calculated as in (6); units of the vertical axis are chosen accordingly.

Figure 1 illustrates different phases in the evolution of phenotypic variance in this process. Environmental variance in this three-allele model depends largely on the frequency of  $A_3$ , and if this allele was started at low frequency, selection favored rapid changes in the frequencies of  $A_1$  and  $A_2$  toward the state  $\bar{z} = z_t^*$ . This initial process was accompanied by large changes in ge-

netic variance (an increase is shown) and little change in environmental variance. However, as  $\bar{z}$  neared the long-term average of  $z_t^*$ , the total phenotypic variance remained fairly constant and the relative proportion of genetic and environmental variance began changing, favoring environmental variance. The rate of increase in environmental variance observed during this latter process varied with the form and parameters of the fitness function, but environmental variance tended to evolve faster with greater temporal variation in the fitness function. Thus, genetic and environmental variance can both be favored in this model, but environmental variance has a small advantage over genetic variance.

#### DISCUSSION

A common practice of evolutionary studies has been to partition the phenotypic variation of a population into genetic and environmental components, the motivation being that these components determine the rate of phenotypic evolution under natural selection (Falconer, 1981; Kempthorne, 1957; Endler, 1986). The present study offered a different perspective on components of phenotypic variation: in those cases where selection actively favors the maintenance of phenotypic variation in a population (recalling that many types of selection reduce variation), genetic and random environmental components may be maintained differentially. Thus, i) selection may be indifferent to the combination of genetic and environmental components (model 3 with constant frequency-dependent selection, and as recognized in many previous studies), ii) selection may favor variation only if it has an environmental component (models 1 and 2 with fluctuating, frequency-independent density-independent selection), or iii) selection may maintain variation of either type alone but favor one component over the other (model 3 with fluctuating frequency-dependent selection).

Environmental effects are themselves not heritable, but the susceptibility to environmental effects is potentially heritable and thus provides a basis for the evolution of environmental variance. Various mutations are known whose expression depends on the external environment during development,

such as temperature-sensitive mutations (Schmalhausen, 1949 pp. 1–22; Lindsley and Grell, 1968), and the phenomenon of partial penetrance or expressivity, discussed in most texts on classical genetics, is a form of environmental variance for discrete characters. The environmental variations of some of these mutations are appropriately regarded as phenotypic plasticity, but the models require only that the variance be independent of the environmental factors causing fluctuations in fitness. Thus a temperature-sensitive mutation might exhibit random environmental variance according to other external factors affecting fitness.

*Bet Hedging: Selection of Environmental Variance?*—A result common to all models above is that fluctuating selection, if sufficiently strong, favors (random) environmental variance in phenotype. Several previous studies concluded that temporally variable selection favors phenotypic variance (bet hedging: e.g., Real, 1980; Caswell, 1983; Kaplan and Cooper, 1984). In other cases authors indicated explicitly or implicitly, that variable selection favors environmental variance in phenotype. Thus Horn (1969), in discussing the possible selected maintenance of color-pattern variation in a snake, used a simple optimization argument to show that strictly alternating environments, first favoring one phenotype and then favoring the other, selected “sibling” or within-family polymorphism rather than between-family polymorphism. Arthur et al. (1973), after observing a low heritability of germination time in a poppy, argued intuitively that the advantage of variance in germination time not only applied to the population but equally applied to a genotype; thus a single, optimal genotype would prevail, and all variance would be environmental. As detailed above, Slatkin and Lande’s (1976) version of model 1 demonstrated evolution of environmental variance under fluctuating selection. Bulmer (1984), in elaborating Cohen’s model of selection for seed dormancy, specifically claimed that bet hedging favored environmental variance, whereas frequency-dependent selection was often indifferent to the type of variance maintained. Finally, Silvertown (1985) and Ellner (1985a) both implied that fluctuating selection favored en-

vironmental variance in germination time (variance within the progeny of one parent), although Ellner’s impressive list of tests of his models (1985b) did not include evaluating components of variance.

In view of the similar predictions from different models, it may seem useful to elevate Bulmer’s statement to the status of a conjecture—that fluctuating selection, if sufficiently strong, favors environmental variance in phenotype. The maintenance of genetic variance is not precluded by fluctuating selection (e.g., Karlin and Liberman, 1974, 1975), but none of the cases studied seems to indicate that fluctuating selection itself favors genetic variance. Rather, the maintenance of genetic variance under fluctuating selection may stem from genetic constraints or the inclusion of other types of selection.

*Empirical Tests: Seed Germination.*—Whenever particular selection regimes are found to favor one class of phenotypic variation over others, empirical tests of the models are offered by the mere analysis of components of phenotypic variance in natural populations. In many cases, the nature of selection may remain so intractable that such tests are not feasible. One fruitful avenue of study along these lines, however, concerns diapause and dormancy. Many plants and animals assume a specialized morphological and physiological state to shelter themselves from seasonally harsh conditions, as in dormant seeds, spores, eggs, and pupae. With the anticipated onset of favorable conditions, these life-forms undergo major, irreversible changes to develop into subsequent stages of the life history. This transition to the new life-form may not be synchronous within a cohort, however: among the seeds of an “annual” plant produced in one year, some are likely to germinate the next year, others the year after, and so forth (Harper, 1977). Similarly, a brood of moth pupae may eclose over a period of months or years (Dingle, 1978), and the diapausing eggs of annual fish resume development at different times (Wourms, 1972).

The case of seed germination offers perhaps the most thorough test at present. Silvertown (1985 p. 146) listed several studies that compared the relative fitness of early

versus late germinators. These studies collectively support the hypothesis that early germination is risky to survival, differentially between years, but early germinators who survive have much higher fecundity than late germinators.

In turn, inheritance of germination time has been reported in a poppy, *Papaver dubium* (Arthur et al., 1973) and a wild snapdragon, *Collinsia verna* (Kalisz, unpubl.). The findings of both studies support the present theory. In *Papaver*, approximately half of the seeds germinated without a winter dormancy. Severe winters usually killed plants that germinated in autumn, whereas mild winters permitted up to 80% of them to survive. These surviving plants had 40 to 80 times the fecundity of spring-germinated plants. A very low heritability of germination time, not significantly different from zero, was noted by these authors, and they in fact offered a verbal explanation for the low heritability along the lines of the present framework. The low heritability of course indicates that most of the phenotypic variance was either environmental (as the models predict) or nonadditive genetic variance; the evidence does not enable discrimination of these two possibilities.

Kalisz (unpubl.) studied germination time in the winter annual plant *Collinsia verna*. In this species, plants germinate during late summer into winter, and early germinators face the hazard of dying as a result of desiccation in years with extended summer (Kalisz, pers. comm.). Kalisz demonstrated that the heritability of germination time was very low and not significantly different from zero. Germination time is best regarded as a continuous variable in this species, and León (1985 p. 138) solved the general optimal germination strategy for this case as a function of the relevant fitness considerations. Just as in model 2 above, genetic variance is not favored in this continuous-character model because of the assumptions of density-independent and frequency-independent selection, hence her results support the theory. (In general, the continuous-character case admits the possibility of selective equivalence of a limited set of different strategies, but genetic variation will at best be selectively neutral.)

In the two years of her study, Kalisz

(1986) observed strict directional selection in favor of early germinators, an observation that is relevant to the models predicting low heritability of germination time. If we consider the distribution between years of  $\tau$ , the earliest date at which germinating seeds will not encounter a systematically fatal environment, León showed that, under a wide range of fitness functions, no seeds are expected to germinate earlier than the modal date of  $\tau$  (assuming that the distribution of germination time is free to take on any form). Thus the event of two consecutive years of directional selection on germination date is not improbable under this model.

*Limitations of the Models.*—The present models incorporated many simplifying assumptions about selection, population structure, and inheritance; a brief review of some previous studies may reflect on the robustness of the models to modifications of these assumptions. A major omission in the present study was the failure to consider mutation. Although the emphasis here was on the selected maintenance of variation, mutation can account for the maintenance of genetic variation when none is favored, and the magnitude of this effect is important in testing the models. Other possible elaborations of the present models were illustrated by Slatkin (1978), who studied the equilibration of polymorphisms under varying assumptions of inheritance and population structure. Evolution to the phenotypic equilibria occurred under various sets of assumptions, but in some cases, temporal changes in population sizes prevented the attainment of equilibria. The incorporation of density effects in the present models might therefore lead to outcomes other than those described here. The use of haploid genetics may also be criticized. Temporal variation in fitness with discrete generations cannot maintain genetic variance (Dempster, 1955; Gillespie, 1973), but genetic variation can be maintained either with haploids and overlapping generations or with diploids and discrete generations (Chesson, 1985; Haldane and Jayakar, 1963; Karlin and Liberman, 1974).

The present study focused on the evolution of genetic versus random environmental variance in phenotype, in which the vari-

ance was expressed between individuals. The evolution of phenotypic variance has been considered in a parallel fashion for other types of environmental variance, particularly for phenotypic plasticity (Via and Lande, 1985; Lloyd, 1984) and for between-versus within-individual variance (the "mixed" strategies of game theory; Maynard Smith, 1982 p. 185; Thomas, 1984). Many biological problems may involve several types of environmental variance rather than just one type, and further models will need to be studied. In general, the rigorous application of models to empirical problems concerning the evolution of phenotypic variance may benefit from investigating a variety of models that incorporate various levels of assumptions deemed realistic by the empiricist.

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APPENDIX I

*Evolutionarily Stable Levels of Environmental Variance for a Multivariate Character*

Text solution (5) for model 1 of a fluctuating optimum will be extended here to consider a multivariate continuous character. The objective is to derive an optimal "environmental" covariance matrix for a set of characters subjected to fluctuating selection. This problem recognizes a parallel in the phenomenon of correlation pleiades, whereby certain suites of characters in an individual are highly correlated among themselves, but uncorrelated with other characters. Berg (1960) proposed that selection favored pleiades to enable sets of characters to operate as functional units amid variation in size of the characters (as in the integration of different parts of the same flower). The analysis of optimal correlation pleiades is therefore the analysis of an optimal covariance structure among multiple characters, conditioned on specific variances in the characters. The present problem is instead the solution of optimal variances as well as covariances.

One method of obtaining a solution is to proceed as in steps (3)-(5) in model 1, with appropriate substitutions of vectors and matrices. Such a maximization procedure proves very cumbersome. An alternative method, suggested to me by Russ Lande, is to transform the multivariate system into a set of independent characters so that solution (5) can be used on each component in the transformation.

Define  $x$  as a  $n \times 1$  vector whose entries represent an individual's phenotypic value for each of  $n$  characters.  $x$  follows a multivariate normal distribution within a genotype with mean  $\mu$  and phenotypic variance matrix  $\Sigma_x$ , non-singular. Genotype-dependence

of these parameters is assumed, but notation indicating genotype-dependence is unnecessary in this appendix and so is omitted. Individual values of  $x$  are subjected to stabilizing selection within generation  $t$  according to a multivariate Gaussian function with optimum  $\bar{p}_{x,t}$  and selection "curvature"  $\Omega_x$ , non-singular and constant in time. Finally,  $\bar{p}_{x,t}$  varies between generations with mean  $\bar{p}_x$  and non-singular variance-covariance matrix  $\Pi_x$ .

The method consists of finding a linear transform of  $x$ ,  $y = Ax$ , so that the corresponding matrices governing selection of  $y$  ( $\Omega_y$ ,  $\Pi_y$ ) are both diagonal. The ESS mean and variance for each element of  $y$  may then be solved independently of the other elements in  $y$ , and the optimal phenotypic variance matrix  $\hat{\Sigma}_y$  is then back-transformed to obtain the optimal means and optimal variances/covariances for  $x$ . Proceeding,

$$\begin{aligned} \hat{\mu}_x &= A^{-1}\hat{\mu}_y, \\ \hat{\Sigma}_x &= A^{-1}\hat{\Sigma}_y(A^T)^{-1}, \end{aligned} \tag{A.1}$$

where the superscript "ESS" indicates an ESS value,  $T$  indicates matrix transpose, and  $^{-1}$  indicates matrix inverse.

To proceed, write

$$\Omega_x = M\Lambda M^{-1}, \tag{A.2}$$

where  $\Lambda$  is the diagonal matrix of eigenvalues, and  $M$  is the corresponding matrix of eigenvectors, chosen so that  $|M| = 1$ . Thus,  $M^{-1} = M^T$ , and

$$\Omega_x = (M\Lambda^2)(M\Lambda^2)^T, \tag{A.3}$$

and

$$I = \Lambda^{-1/2}M^T\Omega_x M\Lambda^{-1/2}. \tag{A.4}$$

Next, transform  $\Pi_x$  as

$$\Pi_x^* = \Lambda^{-1/2}M^T\Pi_x M\Lambda^{-1/2} \tag{A.5}$$

and find  $U$  and  $\Phi$  such that

$$\Pi_x^* = U\Phi U^{-1}, \tag{A.6}$$

with  $\Phi$  as the diagonal matrix of eigenvalues for  $\Pi_x^*$ , and  $U$  as the matrix of eigenvectors, with  $|U| = 1$  (hence  $U^{-1} = U^T$ ).

Let

$$A = U^T\Lambda^{-1/2}M^T. \tag{A.7}$$

We have  $A\Pi_x A^T = \Phi$ , the diagonal matrix of eigenvalues for  $\Pi_x^*$ , and

$$A\Omega_x A^T = U^T I U = I, \tag{A.8}$$

(since  $U$  is orthogonal) as required.

This method is easily applied to special cases on a computer, but the simple case in which  $x$  is  $2 \times 1$  and

$$\Omega_x = \omega^2 \begin{pmatrix} 1 & \alpha \\ \alpha & 1 \end{pmatrix}, \Pi_x = \pi^2 \begin{pmatrix} 1 & \beta \\ \beta & 1 \end{pmatrix},$$

can be solved analytically. An appropriate transform is seen to be

$$A = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & 1 \\ -1 & 1 \end{pmatrix},$$

and the solutions for ESS variances,  $\bar{\Sigma}_x$ , are divided into four cases:

- 1) 
$$\begin{pmatrix} \pi^2 - \omega^2 & \pi^2\beta - \omega^2\alpha \\ \pi^2\beta - \omega^2\alpha & \pi^2 - \omega^2 \end{pmatrix}$$
 if  $\gamma_1 > \gamma_2, \gamma_3 > \gamma_4$ ;
- 2) 
$$\begin{pmatrix} 0 & 0 \\ 0 & 0 \end{pmatrix}$$
 if  $\gamma_1 \leq \gamma_2, \gamma_3 \leq \gamma_4$ ;
- 3) 
$$\frac{\pi^2(1 + \beta) - \omega^2(1 + \alpha)}{2} \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}$$
 if  $\gamma_1 > \gamma_2, \gamma_3 \leq \gamma_4$ ;
- 4) 
$$\frac{\pi^2(1 - \beta) - \omega^2(1 - \alpha)}{2} \begin{pmatrix} 1 & -1 \\ -1 & 1 \end{pmatrix}$$
 if  $\gamma_1 \leq \gamma_2, \gamma_3 > \gamma_4$ ;

with  $\pi^2(1 + \beta) = \gamma_1$ ,  $\omega^2(1 + \alpha) = \gamma_2$ ,  $\pi^2(1 - \beta) = \gamma_3$ ,  $\omega^2(1 - \alpha) = \gamma_4$ . The ESS solution  $\hat{\mu}_x$  is given simply by  $\bar{P}_x$ .

## APPENDIX II

### Optimal Environmental Variance of a Polygenic Character

This appendix describes the assumptions and results of a simulation model studied to compare the optimal variance predicted by text expression (5c) with the selection threshold predicted by Slatkin and Lande (1976) for a polygenic character under stabilizing selection with a fluctuating optimum. The simulations modeled a character  $x$  influenced by four bi-allelic loci in an infinite diploid population with discrete, non-overlapping generations;  $x$  was subjected to Gaussian selection with an optimum chosen at random each generation. At each of loci 1–3, alleles were assigned values 0 or 1, and the individual's average value of  $x$

was the sum of values over these three loci; the genotype at the fourth locus specified the environmental variance in  $x$ .

The simulations incorporated the following sequence of events.

- 1) Initial gamete frequencies were assigned. The parameter of stabilizing selection ( $\omega^2$ ), environmental variances [ $\sigma_e^2(k)$ ], and the average optimum value of  $x$  ( $\psi$ ) were set for the ensuing generations.
- 2) Gamete frequencies were altered deterministically by mutation at loci 1–3 only. The probability that an allele 0 mutated to 1 was the same as that from 1 to 0, and the rates were also the same at all three loci. Mutation rates were chosen as 0.001 in most simulations, but rates of 0.002 and 0.005 were also studied.
- 3) Zygotes were formed from gametes paired in proportion to their frequencies with no sex differences. These diploids were subjected to Gaussian viability selection as in text expression (1), with the frequency of each genotype multiplied by the value determined by expression (3), where  $\mu(k)$  was the sum of allelic values over loci 1–3,  $\sigma_e^2(k)$  was the environmental variance determined by the genotype at the fourth locus, and  $\psi$  was calculated as  $\psi$  plus a random variable chosen each generation from a uniform distribution with mean zero and variance  $\pi^2$ .
- 4) Gamete frequencies were calculated deterministically from the survivors assuming free recombination among all loci; these frequencies were then normalized to sum to unity. The process then returned to step (2) to initiate a further generation until a set number of generations had been reached.

For calculation of the heritability of  $x$ , which enters into the Slatkin-Lande threshold, the genetic variance of  $x$  was calculated each generation after mutation in step (2), with each gamete's value of  $x$  as the sum of allelic values over loci 1–3. Under random mating and with no sex differences, the genetic variance of gametes is half that of zygotes, so the variance obtained from gametes was doubled. Genetic variances were averaged over 1,000 generation intervals. The heritability of  $x$

TABLE AII. Evolution of environmental variance in a polygenic character. Sixteen trials of 10,000 generations each were run for each set of parameter values. Alleles  $A$  and  $a$  apply to locus 4, the locus modifying the environmental variance. In all cases, the environmental variance of heterozygotes,  $\sigma_e^2(Aa)$ , was the average of that for  $aa$  and  $AA$ . After 10,000 generations, allele  $A$  was designated "rare" if its frequency was less than 0.01, "common" if greater than 0.99, and "int" (intermediate) otherwise. The value listed for  $\pi^2$  was the expected variance in the optimum, and although the actual variances in the trials differed from expectation, the discrepancies were minor. Symbols (as used in text model 1 also) are as follows.  $\pi^2$ : temporal variance in the optimum of  $x$ ;  $\omega^2$ : parameter of stabilizing selection on  $x$ ;  $h^2$ : heritability of  $x$ ; and  $\sigma_e^2(k)$ : environmental variance in  $x$  produced by genotype  $k$  (the genotype at locus 4).

Parameter values					Outcome		
$\pi^2$	$\pi^2 - \omega^2$	$\pi^2 - \frac{\omega^2}{1 + h^2}$	$\sigma_e^2(aa)$	$\sigma_e^2(AA)$	$A$ rare	$A$ int (number of trials)	$A$ common
0.333	0.083	0.17	0.083	0.103	16	0	0
0.75	0	0.37	0	0.1	16	0	0
0.75	0.05	0.37–0.39	0	0.1	0	16	0
0.75	0.1	0.39	0	0.1	0	9*	7

\* Five of these trials ended with the frequency of  $A$  greater than 0.98.

was then calculated as the ratio of the average genetic variance to the sum of genetic plus environmental variance. The average genetic variance (per 1,000 generations) was essentially constant over the course of each simulation, but the environmental variance often changed substantially, due to selection of alleles at the fourth locus. The calculation of the heritability was therefore based on the environmental variance observed at the end of the trial.

The simulation model was run for several sets of initial conditions and various sequences of random numbers over 10,000 generations each (a representative subset is given in Table AII). The genetic variance of  $x$  maintained during a trial depended on the mutation rate and also depended heavily on the choice of the average optimum,  $\psi$ : if  $\psi$  was odd (3, for example), it could be achieved only by a diploid genotype heterozygous for at least one of loci 1-3, and a much higher level of genetic variance was maintained than if the optimum was even (2 or 4) and could be achieved by

a genotype homozygous for all of loci 1-3. This effect on the genetic variance was therefore simply an artifact of the assumption that alleles at loci 1-3 were restricted to values 0 and 1.

The evolutionary process was often insensitive to small differences in  $\sigma_e^2(k)$ , and it was not generally possible to precisely identify a favored level of environmental variance. However, the results did enable a comparison of the Slatkin-Lande threshold with result (5c), and for those trials in which the two models predict different outcomes, result (5c) seemed to be supported (Table AII). The magnitude of the heritability did not seem to affect the selected level of environmental variance, although the rate of evolution was retarded by the higher levels of genetic variance. Note that the runs in the third row of the table, in which only the heterozygote at locus 4 produced the optimum environmental variance, consistently maintained heterozygosity at locus 4.