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Evolution, Vol. 49, No. 1. (Feb., 1995), pp. 151-163.

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EVOLUTION AND EXTINCTION IN A CHANGING ENVIRONMENT: A QUANTITATIVE-GENETIC ANALYSIS

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Abstract.—Because of the ubiquity of genetic variation for quantitative traits, virtually all populations have some capacity to respond evolutionarily to selective challenges. However, natural selection imposes demographic costs on a population, and if these costs are sufficiently large, the likelihood of extinction will be high. We consider how the mean time to extinction depends on selective pressures (rate and stochasticity of environmental change, and strength of selection), population parameters (carrying capacity, and reproductive capacity), and genetics (rate of polygenic mutation). We assume that in a randomly mating, finite population subject to density-dependent population growth, individual fitness is determined by a single quantitative-genetic character under Gaussian stabilizing selection with the optimum phenotype exhibiting directional change, or random fluctuations, or both. The quantitative trait is determined by a finite number of freely recombining, mutationally equivalent, additive loci. The dynamics of evolution and extinction are investigated, assuming that the population is initially under mutation-selection-drift balance. Under this model, in a directionally changing environment, the mean phenotype lags behind the optimum, but on the average evolves parallel to it. The magnitude of the lag determines the vulnerability to extinction. In finite populations, stochastic variation in the genetic variance can be quite pronounced, and bottlenecks in the genetic variance temporarily can impair the population's adaptive capacity enough to cause extinction when it would otherwise be unlikely in an effectively infinite population. We find that maximum sustainable rates of evolution or, equivalently, critical rates of environmental change, may be considerably less than 10% of a phenotypic standard deviation per generation.

Key words.—Demographic stochasticity, environmental change, extinction, genetic stochasticity, mutation, quantitative genetics, selection.

Received July 13, 1993. Accepted December 1, 1993

Paleontologists have focused a great deal of attention on episodes of mass extinction and the physical factors that might have led to them. More recently, concern with basic factors that determine the vulnerability of small populations to extinction has driven the development of a substantial body of theory in conservation biology. In both of these fields, remarkably little attention has been devoted to understanding the influence of evolutionary processes on the risk of extinction.

Natural selection resulting from temporal environmental change poses a major challenge to all organisms. By causing higher mortality and/or lower fecundity than would occur otherwise, natural selection usually will impose a demographic load on a population by reducing the population growth rate or density, or both. In the short term, populations can meet this challenge by migrating to more favorable habitat (Pease et al. 1989), by acclimating physiologically (Ayres 1993), and in some special cases, by entering diapause. However, in the face of a long-term directional trend in the environment, evolutionary adaptation is essential to population survival (Geber and Dawson 1993; Hoffmann and Blows 1993; Lynch and Lande 1993). Since most populations harbor some genetic variation for most quantitative characters, the potential for evolutionary change is ubiquitous, as demonstrated by numerous long-term programs of artificial selection (Falconer 1989). Less clear is the magnitude of selection that can be sustained by a population before the load is so great that the population begins to decline toward extinction.

Models have been developed that predict a critical rate of long-term environmental change beyond which extinction is certain (Lynch et al. 1991; Lynch and Lande 1993). These models give at least a qualitative picture of the ecological and genetic factors involved in the extinction of populations

facing selective challenges. The models also yield some insight into the constraints on the long-term rate of phenotypic evolution. Since viable populations must ultimately evolve at the same rate as the environment is changing, the critical rate of environmental change is equivalent to the maximum sustainable rate of evolution.

The theory developed in Lynch and Lande (1993) was focused on small sexual populations, but in the interest of simplicity, extinction was treated as an essentially deterministic process. A positive geometric-mean growth rate of the population was used as a criterion for survival. Populations exposed to a rate of environmental change exceeding the critical rate were assumed to be doomed to certain extinction, which is reasonable. However, populations exposed to rates of change below the critical rate were assumed to be immortal, a condition that cannot be strictly valid for finite populations subject to genetic and demographic stochasticity.

Even if the critical rate of change identified by Lynch and Lande (1993) is not exceeded, provided all individuals have a nonzero probability of dying, any population will have some finite probability of becoming extinct in any generation. In principle, this probability may be substantial if the rate of environmental change is below but near the threshold. In a finite population, the genetic variance can drift substantially from generation to generation (Lynch and Hill 1986; Bürger et al. 1989; Keightley and Hill 1989; Zeng and Cockerham 1991), and recovery from periods of low variation can sometimes require a large number of generations. Such temporal bottlenecks in genetic variance can cause a population to lag temporarily so far behind the optimum phenotype that extinction would be highly likely even if unexpected in a deterministic situation. In addition, if the environmental change has a stochastic as well as a directional component, it is

possible that by chance the population will experience a long sequence of particularly extreme environments. This can cause the population rate of growth to be negative for a long enough time to cause extinction, and even if extinction does not result immediately, the loss of genetic variance resulting from a depressed population size can substantially reduce the population's ability to respond to future selective challenges. In principle, these types of synergistic effects could lead to rapid extinction at rates of environmental change much lower than those identified by Lynch and Lande (1993) as critical.

The purpose of this paper is to determine how the expected time to extinction depends on general features of demography (potential rate of population growth), the environment (carrying capacity, forces of selection), and the genetic system (rate of polygenic mutation). Although our approach to the problem departs from that used by Lynch and Lande (1993), the two approaches are related, as even after various sources of stochasticity are accounted for, there is still a rate of environmental change beyond which extinction is virtually certain to occur rapidly.

Our results are based largely on computer simulations, taking into explicit consideration the genetics of the selected trait, allowing for a stochastic component of environmental change, and incorporating a simple model of density-dependent population growth. We also introduce an analytical approach that under a broad range of conditions yields predictions that are in good accord with the simulation results. In addition to yielding information relevant to the extinction process, this study provides some insight into the expected dynamics of the mean and variance of a quantitative trait in a changing environment.

The General Model

We consider a randomly mating, finite population with discrete generations, subject to density-dependent population regulation. Individual fitness is determined by a single quantitative character under Gaussian stabilizing selection on viability, with the optimum phenotype θ_t exhibiting temporal change. The viability of an individual with phenotypic value z is assumed to be

$$W_{z,t} = \exp\left[-\frac{(z - \theta_t)^2}{2\omega^2}\right], \quad (1)$$

where ω^2 is inversely proportional to the strength of stabilizing selection. That is, the curvature of the fitness function near its optimum increases with decreasing ω^2 . Selection acts only through viability selection, and each individual produces B offspring.

Our intention is to investigate the response to environmental change for a population that has been at mutation-selection-drift balance. This environmental change may be either directional, or stochastic, or a combination of both. A simple model for this is a phenotypic optimum that moves at a constant rate k per generation, fluctuating randomly about its expected position,

$$\theta_t = kt + \epsilon_t, \quad (2)$$

where ϵ_t represents white noise with variance σ_ϵ^2 , mean zero, and no autocorrelation. Under this model, the population ex-

periences a mixture of directional and stabilizing selection. Throughout, the width ω of the fitness function is assumed constant.

The quantitative character under consideration is assumed to be determined by n freely recombining, equivalent loci. The allelic effects are additive within and between loci; that is, there is no dominance or epistasis. The phenotypic value of an individual is the sum of a genetic contribution and a normally distributed environmental effect with mean zero and variance $\sigma_\epsilon^2 = 1$. Therefore, the phenotypic mean equals the mean of the additive genetic values, \bar{g}_t , and the phenotypic variance is $\sigma_{z,t}^2 = \sigma_{g,t}^2 + \sigma_\epsilon^2$, with $\sigma_{g,t}^2$ denoting the additive genetic variance in generation t . We shall use the parameter $V_s = \omega^2 + \sigma_\epsilon^2 = \omega^2 + 1$ to describe the strength of stabilizing selection on the breeding values. Assuming that the phenotypes follow a normal distribution (with mean \bar{g}_t and variance $\sigma_{z,t}^2$), the mean viability of the population is

$$\bar{W}_t = \sqrt{\frac{\omega^2}{V_s + \sigma_{g,t}^2}} \exp\left[-\frac{(\bar{g}_t - \theta_t)^2}{2(V_s + \sigma_{g,t}^2)}\right] \quad (3a)$$

(Latter 1970), and its (multiplicative) growth rate is

$$R_t = B\bar{W}_t. \quad (3b)$$

A similar model was developed by Lynch and Lande (1993), Lynch et al. (1991), and Charlesworth (1993), although the latter two focused on populations of infinite size.

We assume the following simple kind of density-dependent population regulation (cf. Lynch et al. 1993). Let K be the carrying capacity, that is, the maximum number of breeding adults. The N_t ($\leq K$) breeding parents in generation t produce BN_t offspring, an expected $R_t N_t$ of which will survive viability selection. In this way, demographic stochasticity is induced. If the actual number of surviving offspring is larger than K , then K individuals are chosen randomly to constitute the next generation of parents. Otherwise, all surviving offspring serve as parents for the next generation. With this type of density-dependent population regulation, the number of reproducing adults remains roughly constant at K , until $\bar{W}_t < 1/B$, at which point the population cannot replace itself.

Analytical Approximations

For a similar continuous-time model, but without density-dependent population regulation, Lynch and Lande (1993) developed a theory of critical rates of environmental change. They defined a critical rate of environmental change, k_c , as that value of k beyond which \bar{W}_t eventually declines below $1/B$. In the present model, extinction is certain, regardless of k , because the number of offspring produced is always finite ($\leq BK$) and there is always a nonzero probability that no offspring survives selection. Thus, our focus will be on the dependence of the mean time to extinction and, to some extent, the distribution of extinction times, on the ecological parameters k , ω^2 , K , B , and σ_ϵ^2 . These parameters (together with genetic parameters like mutation rates, number of loci, etc.) determine the distribution of the quantitative-genetic trait, in particular its mean \bar{g} and its variance σ_g^2 , which in turn defines the mean viability. The derivation of an exact theory for the joint process of evolution and extinction is beyond our capabilities. The following theoretical approach,

based on several simplifying assumptions, is intended primarily as a guide to the qualitative behavior of the general model. Nevertheless, it provides good approximations in some important regions of the parameter space. The first part up to equation (10) is parallel to Lynch and Lande's (1993) treatment, however more general, because our discrete-generation model neither requires weak selection nor small σ_g^2 .

A Gaussian Theory for the Dynamics of the Mean Phenotype.—The evolutionary dynamics of the selected character is key to understanding the extinction process. As a result of directional environmental change, the mean phenotype \bar{g} evolves but lags behind the optimum. Once the mean phenotype lags sufficiently far behind θ that $\bar{W} < 1/B$, the population size starts to decline. With a smaller population size, genetic drift reduces the genetic variance, which leads to an even larger lag of the mean phenotype and a further decrease of mean fitness. Once this synergistic process begins, extinction soon follows. For the rest of this subsection we assume that k and σ_g^2 are small enough, so that \bar{W} is sufficiently high to ensure that the effective population size N_e is approximately constant.

Since stochasticity plays an important role in our model, a theory is needed that makes predictions for an "average" population. In our theory for the probability distribution of mean phenotypes, we will consider the genetic variance to be constant and assume that a numerical or theoretical estimate is available, an assumption that will be discussed later. We will use the notation

$$s = \frac{\sigma_g^2}{\sigma_g^2 + V_s} \quad \text{and} \quad 1 - s = \frac{V_s}{\sigma_g^2 + V_s},$$

where s is a measure for the strength of selection.

Under our assumption of a Gaussian distribution of phenotypic values and a constant genetic variance, the expected dynamics of the mean phenotype, conditional on the given values \bar{g}_t and θ_t , is

$$E[\bar{g}_{t+1} | \bar{g}_t, \theta_t] = \bar{g}_t + s(\theta_t - \bar{g}_t). \quad (4)$$

In fact, the conditional distribution of \bar{g}_{t+1} is Gaussian with mean given by (4) and variance σ_g^2/N_e , where N_e is the effective population size (cf. Lande 1976). Denoting this conditional distribution by f , the unconditional distribution of the mean phenotype by Φ , and the distribution of θ_t by Θ , we obtain the recursion

$$\Phi(\bar{g}_{t+1}) = \int \left[\int f(\bar{g}_{t+1} | \bar{g}_t, \theta_t) \Phi(\bar{g}_t) d\bar{g}_t \right] \Theta(\theta_t) d\theta_t. \quad (5)$$

This generalizes Lande's (1976) equation (16), by including variation of the optimum θ . From equation (5), taking into account (2), the following recursions for the expected mean and the expected variance of \bar{g} are obtained:

$$E[\bar{g}_{t+1}] = E[\bar{g}_t] + s(kt - E[\bar{g}_t]), \quad (6a)$$

$$V[\bar{g}_{t+1}] = \frac{\sigma_g^2}{N_e} + (1 - s)^2 V[\bar{g}_t] + s^2 \sigma_g^2. \quad (6b)$$

From these equations, the dynamics of the expected mean phenotype (with random drift and fluctuations of the optimum

averaged out), and of the variance of the mean phenotype are easily obtained:

$$E[\bar{g}_t] = kt - \frac{k}{s} [1 - (1 - s)^t] + (1 - s)^t E[\bar{g}_0],$$

$$V[\bar{g}_t] = \left[\frac{(\sigma_g^2 + V_s)^2}{N_e(\sigma_g^2 + 2V_s)} + \frac{\sigma_g^2 \sigma_g^2}{\sigma_g^2 + 2V_s} \right] [1 - (1 - s)^{2t}]$$

$$+ (1 - s)^{2t} V[\bar{g}_0] \quad (7a)$$

$$\approx \left[\frac{V_s}{2N_e} + \frac{\sigma_g^2 \sigma_g^2}{2V_s} \right] [1 - (1 - s)^{2t}]$$

$$+ (1 - s)^{2t} V[\bar{g}_0]. \quad (7b)$$

These two formulas correspond to equations (14) and (15) in Lynch and Lande (1993). Together, they define the Gaussian probability distribution for the mean phenotype for populations with genetic variance σ_g^2 exposed to environments with properties k , ω^2 , and σ_g^2 .

The influence of the distribution of initial mean phenotypes becomes weaker as time elapses. Asymptotically, for large t , the distribution $\Phi(\bar{g})$ settles down to a traveling wave with mean and variance given by

$$E[\bar{g}_t] \approx kt - k/s, \quad (8a)$$

$$V[\bar{g}_t] \approx \frac{V_s}{2N_e} + \frac{\sigma_g^2 \sigma_g^2}{2V_s} = V[\bar{g}]. \quad (8b)$$

As noted previously under this model (Charlesworth 1993; Lynch and Lande 1993), the mean phenotype eventually evolves with an expected rate exactly equal to the rate of environmental change k , but lags behind the optimum by an expected amount k/s . Similar phenomena have been found for other forms of directional selection (cf. Hill 1982; Bürger 1993). Assuming a population initially at the environmental optimum, $E[\bar{g}_0] = V[\bar{g}_0] = \theta_0 = 0$, the time scale for approaching this equilibrium is as follows (Lynch and Lande 1993). From (7a), the expected mean phenotype $E[\bar{g}_t]$ attains 95% of its asymptotic value (relative to the optimum), when $(1 - s)^{t_{0.95}} = 0.05$. Provided $\sigma_g^2 \ll V_s$, $t_{0.95} \approx 3/s \approx 3V_s/\sigma_g^2$. The variance of the distribution of \bar{g} equilibrates in approximately half this time.

With the help of equations (7a,b), an explicit formula can be derived for the expected growth rate λ_t of the population at time t . Denoting $V_{\lambda,t} = V_s + \sigma_g^2 + V[\bar{g}_t] + \sigma_g^2$ and taking the expectation of R_t (cf. eqs. 3a,b) with respect to the normal distributions of \bar{g}_t and θ_t , we obtain

$$\lambda_t = BE[\bar{W}_t] = B_{O,t} \exp \left\{ - \frac{(E[\bar{g}_t] - kt)^2}{2V_{\lambda,t}} \right\}, \quad (9)$$

where

$$B_{O,t} = \frac{B\omega}{\sqrt{V_{\lambda,t}}}$$

is the expected growth rate if $E[\bar{g}_t] = kt$. By assumption, we always have $\bar{g}_0 = 0$ initially, so that $\lambda_0 = B_{O,0}$. By analogy with Lynch and Lande (1993), the critical rate of environmental change k_c is defined as the value of k such that the population can just replace itself, that is, such that $\lambda_\infty = 1$. A simple calculation shows that

$$k_c = \frac{\sigma_g^2}{\sigma_g^2 + V_s} \sqrt{2V_\lambda \ln B_O}, \quad (10)$$

where $V_\lambda = V_{\lambda, \infty}$ and $B_O = B_{O, \infty} = B\omega/\sqrt{V_\lambda}$. Equation (10) agrees with equation (10) of Lynch and Lande (1993) in the limit of large ω^2 and small σ_g^2 .

Formula (10) is deceptively simple because we have not elucidated the determinants of the genetic variance yet. The genetic variance σ_g^2 depends on the width of the fitness function, the number of loci, the effective population size, the mutation parameters, and, unless the distribution of breeding values is exactly Gaussian, on the rate of environmental change k . Thus, an exact solution of equation (10) requires a priori knowledge of σ_g^2 for $k = k_c$. The dependence of σ_g^2 on the various parameters is investigated in some detail in a section below.

A Quasi-Deterministic Approximation for the Mean Time to Extinction.—The preceding theory predicts that a population will survive and evolve towards a steady response, as given by (8a), if $k \leq k_c$. Otherwise, it will decline towards extinction, despite any ability to evolve. To obtain a kind of “quasi-deterministic theory” of extinction times for the case in which the critical rate has been exceeded, we assume that the expected growth rate λ_t describes the dynamics of the population size with reasonable accuracy. Two phases of population dynamics need to be considered. During the first phase, λ_t declines steadily until $\lambda_t = 1$, with the number of reproductive adults remaining constant at K (we assume that $N(0) = K$). Let t_1 denote the length of this phase. During the second phase, as λ_t decreases further, the population size progressively declines. We define extinction as having occurred when the population size has been reduced to a single individual (this is clearly justified in dioecious species). Denoting the length of the second phase by t_2 , the mean time to extinction is $\bar{t}_e = t_1 + t_2$.

In the following equation, we assume for simplicity that $V_{\lambda, t}$ is approximately constant, and equal to V_λ . This is justified under the weak assumption that $\sigma_g^2 + V[\bar{g}_t] \ll V_s + \sigma_g^2$. Then, a surprisingly simple formula can be derived for the length of the first phase. We have only to solve equation (9) for t such that $\lambda_t = 1$. To this aim, let

$$k = \kappa k_c, \quad \kappa > 1.$$

A straightforward calculation, using equations (7a), (9), and (10), shows that

$$\lambda_t = B_O^{1-\kappa^2} [1 - (1-s)^t]^2. \quad (11)$$

Provided $B_O > 1$ (i.e., the population would be capable of positive growth if the mean phenotype coincided with the optimum), the length t_1 of phase one, is obtained by solving equation (11) with $\lambda_t = 1$,

$$t_1 = \frac{\ln(1-1/\kappa)}{\ln(1-s)} \approx -\frac{\sigma_g^2 + V_s}{\sigma_g^2} \ln\left(1 - \frac{k_c}{k}\right), \quad (12a)$$

for $k > k_c$.

If k_c/k is sufficiently small, so that $\ln(1 - k_c/k) \approx -k_c/k$, we obtain from equations (12a) and (10) the approximation

$$t_1 \approx \frac{1}{k} \sqrt{2V_\lambda \ln B_O} \quad \text{for } k \gg k_c. \quad (12b)$$

The derivation of equations (12a,b) assumed σ_g^2 to be independent of k and of time. Although this is not the case in our model, equation (12a) can be applied if the right-hand side of equation (10) is substituted for k_c , but with σ_g^2 as observed or estimated by the average genetic variance for the given k . Equation (12b) shows that t_1 is approximately independent of the population size and of the genetic variance.

No closed formula is available for the length t_2 of the second phase. However, the recursion $N_{t+1} = \lambda_t N_t$, with initial condition $N_0 = K$ and λ_t defined by equation (9), is easily iterated on a computer until N_t reaches one. In most, but not all, cases, the second phase is shorter than the first phase. From the above recursion it can be seen that t_2 is approximately proportional to $\ln K$ if $k \gg k_c$. Since t_1 is approximately independent of K , \bar{t}_e increases more slowly than $\ln K$. This is not too surprising because the condition $k \gg k_c$ is equivalent to $\lambda_t \ll 1$, and it is well known from models of environmental stochasticity that, even without genetic stochasticity, the mean time to extinction scales as $\ln K$ (Lande 1993).

Since this quasi-deterministic theory neglects several sources of stochasticity (fluctuations of R_t about its mean λ_t , demographic stochasticity, stochasticity, and autocorrelation resulting from genetic events like mutation and recombination), it will always overestimate \bar{t}_e . In particular, extinction also will occur (with probability one) at rates of environmental change less than k_c . Taking into account variation of R_t (resulting from genetic stochasticity and environmental fluctuations), and replacing the expected growth rate λ_t by the smaller long-run growth rate (cf. Lewontin and Cohen 1969; Lande 1993) yields only slightly lower estimates of the critical rate and of the mean extinction time if $\sigma_g^2 = 0$. Therefore, we refrain from presenting such approximations.

The Simulation Model

Because the basic model is very complex, combining temporally variable aspects of the environment with a quantitative-genetic model based on polygenic inheritance, comprehensive stochastic computer simulations have been performed to determine the dynamics of evolution and extinction more explicitly and to check the analytical approximations. The simulation model has been adapted from the one used in Bürger et al. (1989) for investigating mutation-selection-drift balance.

The genotypic value of the character is determined by n additive loci with no dominance or epistasis. We chose $n = 50$ for all of our simulations. We simulate the continuum-of-alleles model of Crow and Kimura (1964) by drawing individual allelic effects from a continuous distribution, so the number of possible segregating alleles per locus is unlimited. The phenotypic value of an individual is obtained from the genotypic value by adding a random number drawn from a normal distribution with mean zero and variance $\sigma_g^2 = 1$. The generations are discrete, and the life cycle consists of three stages, as described below.

To initialize the simulation, a population of K parents is generated by choosing five allelic effects at each locus and randomly sampling alleles such that a binomial distribution

with given variance is obtained; subsequently, the population is allowed to evolve under stabilizing selection until it reaches mutation-selection-drift balance, as judged by means of the stochastic house-of-cards approximation developed in Bürger et al. (1989). The parameters during this phase are identical to those during the phase of environmental change to follow, except that $k = 0$ and $\sigma_0^2 = 0$.

1. *Population Regulation and Random Sampling of Breeding Pairs.*—The surviving offspring of the preceding generation form the potential breeding pool. If, at this point, the number of individuals is K (= carrying capacity) or less, then all individuals (with the possible exception of one, because of monogamy) serve as parents for the next generation, and the appropriate number of breeding pairs is formed. Otherwise, K individuals are sampled without replacement to constitute the next generation of parents. The sex ratio is always 1:1. Thus, the mating system is dioecious and monogamous.

2. *Production of Offspring.*—We assume that there are neither differences nor stochasticity in fertility or fecundity. Each breeding pair produces the same number of offspring, namely $2B$. The genotype of each descendant is obtained from that of its parents, with free recombination and alleles subject to mutation with genic mutation rate μ . For each gamete, a uniformly distributed random number between 0 and 1 is drawn, and if this random number is lower than the gametic mutation rate $n\mu$, one of the genes constituting this gamete is chosen randomly for a mutation to occur (since in our simulations $n\mu = 0.01$, the probability that an individual incurs more than one mutant at a locus is negligible). The effect of the new allele is obtained by adding a Gaussian random number with mean zero and variance α^2 to the current allelic effect. In the present simulations, we assumed $\mu = 2 \times 10^{-4}$, and $\alpha^2 = 0.05$. This gives a genomic mutation rate of $2n\mu = 0.02$ and an input of mutational variance per generation of $V_m/\sigma_e^2 = 10^{-3}$, as approximately observed in empirical studies (Lande 1976; Lynch 1988).

3. *Viability Selection.*—Selection acts solely through viability selection before reproduction. This was imposed by assigning the fitness $0 < W_{z,t} \leq 1$ (according to formulas [1] and [2]) to individuals of type z . The survivors, determined by drawing uniformly distributed random variables, served as the potential breeding pool for the next parental generation as described above. By this means, viability selection induces demographic stochasticity.

This life cycle was iterated until extinction occurred, that is, until one or no individual survived selection. All of the statistics on the quantitative trait and fitness were evaluated after reproduction but before selection.

Since each breeding pair produces exactly $2B$ offspring and, in the absence of selection, N parents are sampled without replacement from the pool of BN potential parents, the family size follows a hypergeometric distribution with mean 2 (the population replaces itself) and variance

$$2 \left(1 - \frac{2}{2B}\right) \left(1 - \frac{2B-1}{BN-1}\right).$$

It follows (Falconer 1989, eq. 4.7) that the effective population size is approximately

$$N_e \approx \frac{2B}{2B-1} N, \quad (13)$$

provided $1/B$ is small compared to N .

A Moving Optimum

To study the influence of the various ecological and genetic parameters on the distribution of extinction times, 100 replicate runs (with different initial populations—resulting from different random seeds) were performed for each parameter combination. The statistics reported below are averages of the data of these 100 replicates.

In order to apply our theoretical approximations, estimates for the effective population size N_e and the additive genetic variance σ_g^2 are needed. Simulations show that formula (13) provides an excellent approximation for N_e in the parameter range we have explored, unless selection is very strong. Moreover, N_e enters the formulas only through $V[\bar{g}_t]$ which is, in general, small compared to V_s , so that deviations from (13) can be neglected.

Obtaining theoretical estimates of σ_g^2 is much more troublesome. In Bürger et al. (1989), it was shown that for stabilizing selection with a fixed optimum, the so-called stochastic house-of-cards approximation

$$\sigma_g^2(\text{SHC}) = \frac{4n\mu\alpha^2 N_e}{1 + \frac{\alpha^2 N_e}{V_s}} \quad (14)$$

provides a good estimate for the additive genetic variance under mutation-selection-drift equilibrium (see also Keightley and Hill 1988; Barton 1989; Houle 1989). The present simulations, with $k = 0$ and $\sigma_0^2 = 0$, confirm this (cf. fig. 6 below). In fact, equation (14) is half the harmonic mean of the deterministic house-of-cards approximation (Turelli 1984) and the neutral prediction

$$\sigma_g^2(N) = 4n\mu\alpha^2 N_e = 2V_m N_e \quad (15)$$

(Lynch and Hill 1986). As long as N_e is less than 500 or so, and stabilizing selection is not too strong (e.g., $V_s \geq 10$), (14) is close to (but less than) (15).

As we shall see below, with a moving optimum the average additive genetic variance always remains below (15), but above (14). This implies that for small-to-moderate population sizes, and with moderate-to-weak stabilizing selection, (14) may be used as a reasonable approximation, regardless of k . If the neutral prediction (15) is used in connection with the quasi-deterministic theory, we obtain an upper limit to \bar{t}_e .

In the following subsections, we show how the extinction dynamics depend on the various ecological parameters. For the rest of this section, we assume $k > 0$ and $\sigma_0^2 = 0$.

Strength of Stabilizing Selection and Extinction Time.—With a fixed optimum ($k = 0$), the mean fitness of a population increases with increasing ω (decreasing selection), and the mean extinction time is expected to increase with ω as well. With a moving optimum, the situation is more complicated. If stabilizing selection is weak (ω large), the fitness function is flat, and the expected lag (see [7a], [8a]) tends to be large. On the other hand, the additive genetic variance σ_g^2 depends

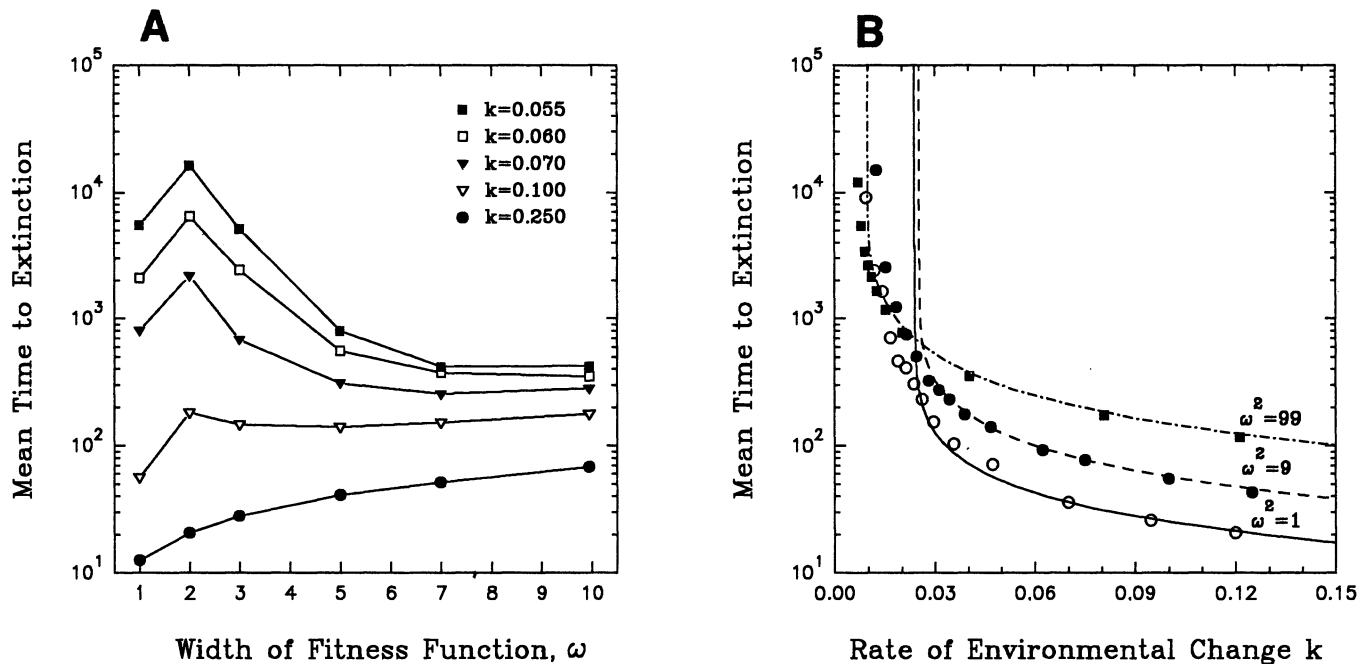


FIG. 1A. Mean time to extinction as a function of the strength ω of stabilizing selection, for different rates of environmental change k . The symbols are averages over 100 replicate simulation runs, as described in the text. The carrying capacity is $K = 128$; the number of offspring produced per individual is $B = 2$; and there are no random fluctuations in the environment ($\sigma_g^2 = 0$). 1B. Mean time to extinction as a function of the rate k of environmental change for weak ($\omega^2 = 99$), moderate ($\omega^2 = 9$), and strong ($\omega^2 = 1$) stabilizing selection. $K = 32$, $B = 2$, and $\sigma_g^2 = 0$.

on ω^2 , that is, for extremely strong selection ($\omega^2 \rightarrow 0$), σ_g^2 tends to zero, whereas for large ω^2 , it becomes almost independent of ω^2 and tends to the neutral expectation (15). Since the response to selection is approximately proportional to σ_g^2 , this suggests \bar{t}_e might be maximized at an intermediate ω^2 , a pattern that is predicted if one substitutes the SHC-approximation (14) for σ_g^2 into formula (10), and plots k_c as a function of ω . The above explanation is slightly different from that of Huey and Kingsolver (1993) who found a maximum k_c at an intermediate ω^2 under the assumption that σ_g^2 is independent of ω^2 .

Figure 1A shows the dependence of the mean extinction time (from stochastic simulations) on the strength of stabilizing selection for various values of k . For high k , we observe that the extinction time increases as the strength of stabilizing selection decreases. For lower k -values (near k_c), we observe a maximum at intermediate ω values.

Figure 1B shows how the mean time to extinction depends on the rate of environmental change k , for three values of ω^2 . The symbols are obtained from numerical simulations, whereas the curves are obtained from the quasi-deterministic approximation of \bar{t}_e together with the assumption that σ_g^2 can be approximated by the SHC-formula (14). The curves become vertical as k approaches the respective k_c values (10) ($k_c = 0.0099$, 0.025 , and 0.024 , for $\omega^2 = 99$, 9 , and 1 , respectively) since the quasi-deterministic approach predicts $\bar{t}_e = \infty$ for $k \leq k_c$. Notice that k_c reflects the expected qualitative dependence of the extinction time on ω^2 noted above— k_c is maximized at an intermediate ω^2 . Again, we see that for large k the mean time to extinction is higher for weaker selection, but not so for low k .

As already pointed out, extinction also occurs when $k < k_c$ because of variation of the growth rate and the genetic variance, stochastic selection, and population regulation. However if $k \ll k_c$, so that the viability stays well above $1/B$, extinction will occur only after an extremely long time, unless the carrying capacity is very low.

Population Size and Extinction Time.—In the face of a changing environment, larger population size reduces the risk of extinction due to stochastic genetic events. However, this effect is not necessarily very large. For sufficiently high values of k , so that the mean growth rate $\lambda < 1$, the extinction risk for large populations is only slightly below that of small populations (fig. 2A). In fact, we demonstrated below formula (12b) that in this case \bar{t}_e increases more slowly than $\ln K$. Given the (reasonable) assumption that the genetic variance does not increase indefinitely as K increases, it is easily seen from equation (10) that k_c asymptotically approaches a constant value as K tends to infinity. This suggests that for sufficiently large k , any population, however large, will become extinct rapidly, whereas for smaller k , the extinction risk for large populations may be significantly lower. This conclusion is supported by figure 2.

Figure 2B displays the dependence of the mean time to extinction on k for three different population sizes, and compares the simulation results with the quasi-deterministic theory. Also, it shows that the advantage of large population size is much more pronounced at smaller rates of environmental change. The curves in figure 2 are based on the quasi-deterministic approximation, with the genetic variance assumed to be given by equation (14). For small k , the larger the population size, the poorer is the approximation. Two

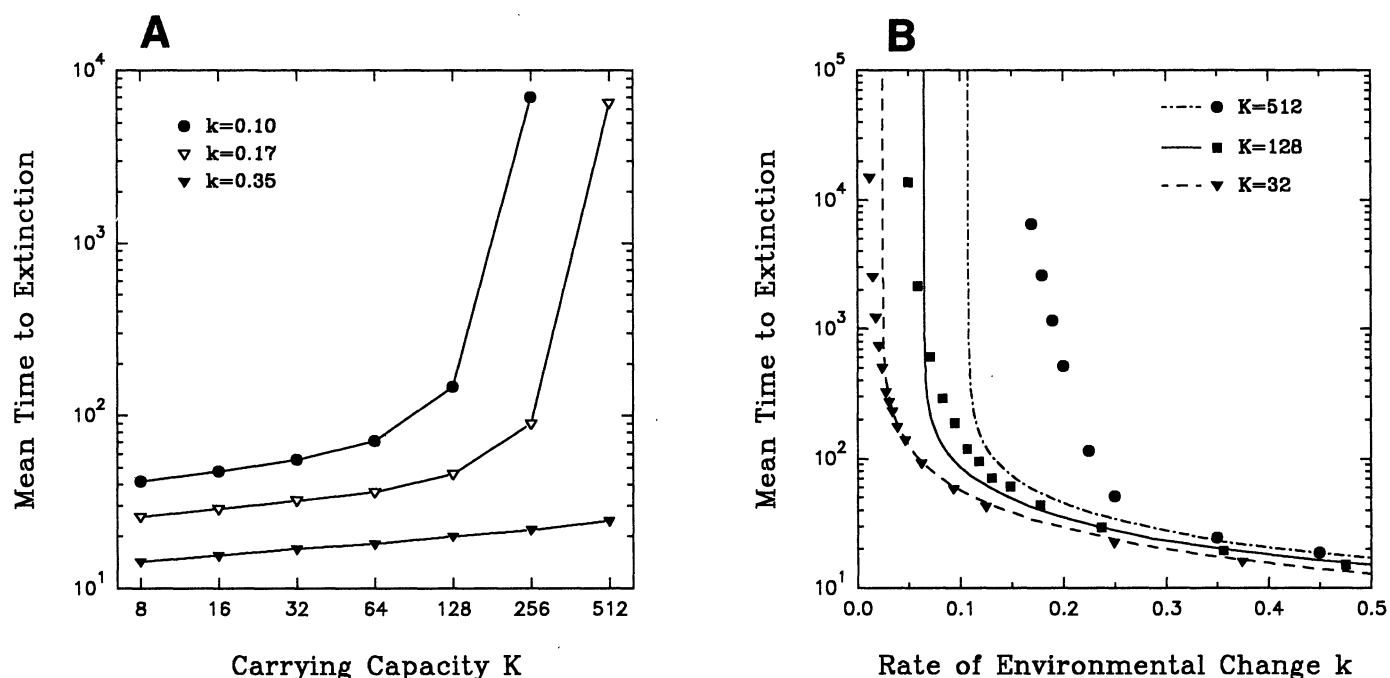


FIG. 2A. Mean time to extinction as a function of the carrying capacity K , for different rates of environmental change k . For all data in both panels, $B = 2$; $\omega^2 = 9$; and $\sigma_g^2 = 0$. 2B. Mean time to extinction as a function of the rate k of environmental change for different carrying capacities. The symbols are data obtained from simulations. The lines indicate mean extinction times from the quasi-deterministic approximation based on the SHC-approximation (14) for the genetic variance (see the text). For $k = 0.45, 0.35, 0.225$, the mean time to extinction, based on numerical estimates of σ_g^2 , is 20, 26, 131, respectively. The observed values are 18.7, 24.6, and 115.5, respectively.

opposing “forces” cause the failure of this approximation. First, the genetic variance is higher than (14) because of directional selection. The magnitude of this effect increases with population size (see fig. 6), leading to a significant increase of k_c and to a higher extinction time, compared to the prediction. Second, as already discussed, the quasi-deterministic approach neglects several sources of stochasticity that decrease the time to extinction. As may be seen from figure 2, which of these forces is stronger depends on the parameters (here on K). For $K = 512$ and the variance taken from (14), the critical rate $k_c = 0.108$ (fig. 2B) is an underestimate because (14) underestimates the observed σ_g^2 . With $\sigma_g^2 = 0.62$, the simulation value obtained for $k = 0.225$, we obtain $k_c = 0.210$ which is an overestimate as expected, because several sources of stochasticity have been neglected. This suggests that random fluctuations of the genetic variance and demographic stochasticity add considerably to the risk of population extinction, whereas increase of genetic variance in response to directional selection decreases the extinction risk.

Number of Offspring and Extinction Time.—The dependence of the mean extinction time on the number B of offspring produced per individual is not simple. If $B \gg \sqrt{V_c}/\omega$ (so that the risk of extinction is very low if the mean phenotype is at the optimum, cf. [9]), we obtain from (10), $k_c \propto \sqrt{\ln B}$. In general, if $k \gg k_c$, equation (12b) implies that $t_1 \propto \sqrt{\ln B}$ and that t_2 depends only weakly (approximately logarithmically) on B . On the other hand, if B is such that the corresponding critical rate is only slightly below the actual rate k , a small increase in the birth rate B may lead to

a significant reduction of the extinction risk because k_c may increase above k . Additionally, given our mating system with monogamy and no variability in fecundity, a larger B leads to smaller N_e and σ_g^2 , thus partially offsetting the reduction of extinction risk gained through increased B .

Distribution of Extinction Times.—As long as extinction occurs quickly, that is, k is well above k_c , the standard deviation of the extinction times is a fraction of the mean. As k becomes smaller, the distribution of extinction times becomes very broad with the standard deviation typically near or even above the mean time to extinction. The median and mode may be significantly lower than the mean, and the range of extinction time may be measured in orders of magnitude (figs. 4A,B). As a consequence, conclusions about the fate of a single population cannot be drawn with confidence from the knowledge of the mean time to extinction, unless the environment changes rapidly.

Stronger stabilizing selection leads to a higher coefficient of variation. The reason seems to be that with strong stabilizing selection, random fluctuations of the mean phenotype may easily lead to extinction, because an unusually large lag leads to a severe decline of fitness.

Dynamics of Extinction.—If k is large, then extinction occurs, more or less, deterministically. The optimum starts to move, and the population mean responds evolutionarily, but the lag becomes larger and larger until the growth rate of the population becomes less than one, and the population size starts its decline towards extinction. In this case, the quasi-deterministic approximation works well.

For k values near or somewhat below the critical rate, the

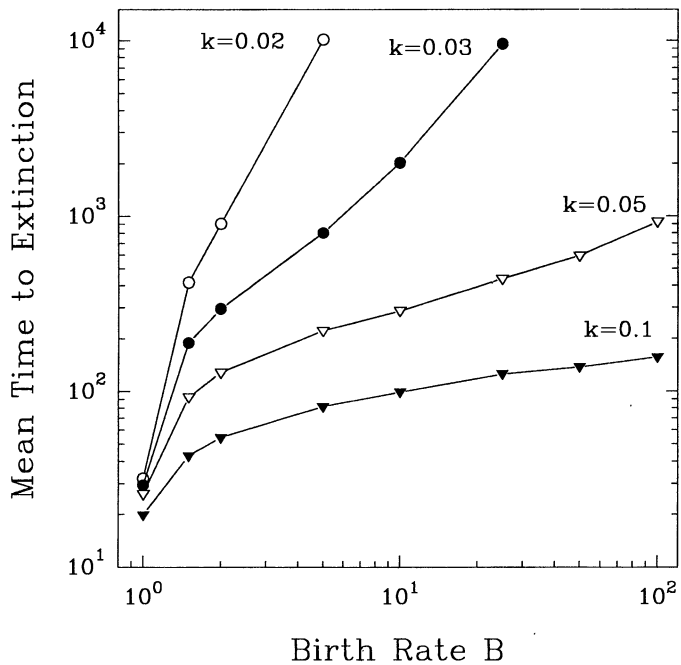


FIG. 3. Mean time to extinction as a function of the number of offspring produced per individual. For all curves, $K = 32$, $\omega^2 = 9$, $\sigma_g^2 = 0$. For $B = 2, 5, 10$, and 100 , the critical rates k_c are 0.025 , 0.039 , 0.047 , and 0.067 , respectively.

situation is more complicated. As discussed in the previous section, the variance among runs can be very large. Some populations simply become extinct in the same way as described above. Others persist for a long time, presumably because favorable mutants occur in time to maintain a high level of variation. This allows the mean phenotype to catch up with the optimum and to follow it more closely for some time. Figure 5 displays one run where the genetic variance gets several boosts because of stochastic mutation events. It also shows the interplay between genetic variance, lag of the mean, and number of survivors of viability selection. When σ_g^2 is high, the lag is low, and the population maintains a high density. (The majority of runs with the same parameters, not displayed, show less “periodicities.”) Figure 5 suggests a high serial correlation for the genetic variance, the lag of the mean phenotype, and the mean fitness. Such correlation has been observed earlier for different forms of selection (Keightley and Hill 1983; Bürger et al. 1989; Bürger et al. 1994).

Once the genetic variance becomes low, the population lag becomes larger and larger. This leads to stronger selection, to a decrease of effective population size, and as a consequence of random genetic drift, to a further decline in genetic variance. If no mutant occurs in time to increase the value of the trait, then the population is doomed to extinction. This kind of synergistic interaction (positive feedback) between population size and fitness decline has been called a “mutational meltdown” in a somewhat different context (Lynch and Gabriel 1990), and seems to be the main reason that extinction is more likely than predicted from our simple theory.

Evolution in Response to Environmental Change.—If the

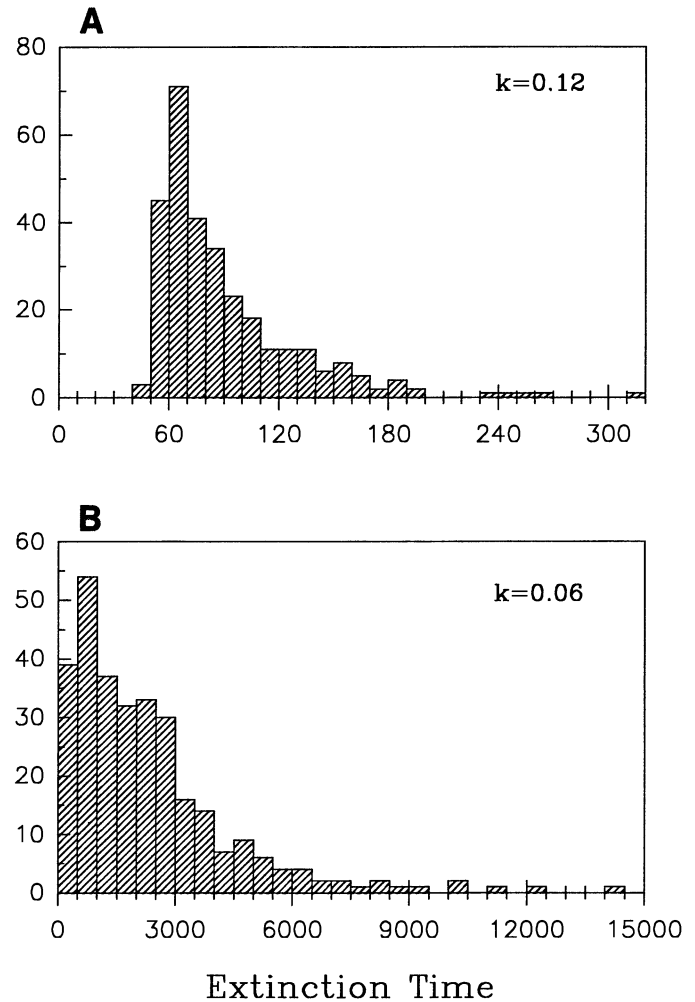


FIG. 4. Probability distribution of the extinction time. Each histogram is based on 300 replicate runs, and for both panels $B = 2$, $K = 128$, $\omega^2 = 9$, and $\sigma_g^2 = 0$. For the upper panel, k is above the critical rate $k_c \approx 0.08$. For the lower panel, k is below. 4A. The average extinction time (over all 300 runs) is $\bar{\tau}_e = 90.6$. The minimum and maximum observed extinction times are 47 and 313 generations, respectively. 4B. $k = 0.06$, $\bar{\tau}_e = 2307.6$, and the maximum and minimum observed extinction times are 120 and 14,015 generations, respectively.

rate of environmental change k is sufficiently low, populations are able to respond evolutionary for a very long time. The results reported below are for rates of environmental change such that no population became extinct within the first 5000 generations.

For the dynamics of the expected mean phenotype $E[\bar{g}_t]$ and the expected variance of the mean phenotype $V[\bar{g}_t]$, we have a simple theory (eqs. 7, 8). Our simulations show that equations (7a) and (8a) describe the evolution of the average mean phenotype adequately, if we insert the observed genetic variance into (7a) and (8a), although the predictions tend to underestimate the observed lag by up to 15% (results not shown). Given all of the simplifications on which this theory is based, this agreement is surprisingly good.

On the other hand, equations (7b) and (8b) yield very poor estimates for the observed variance of the mean phenotype,

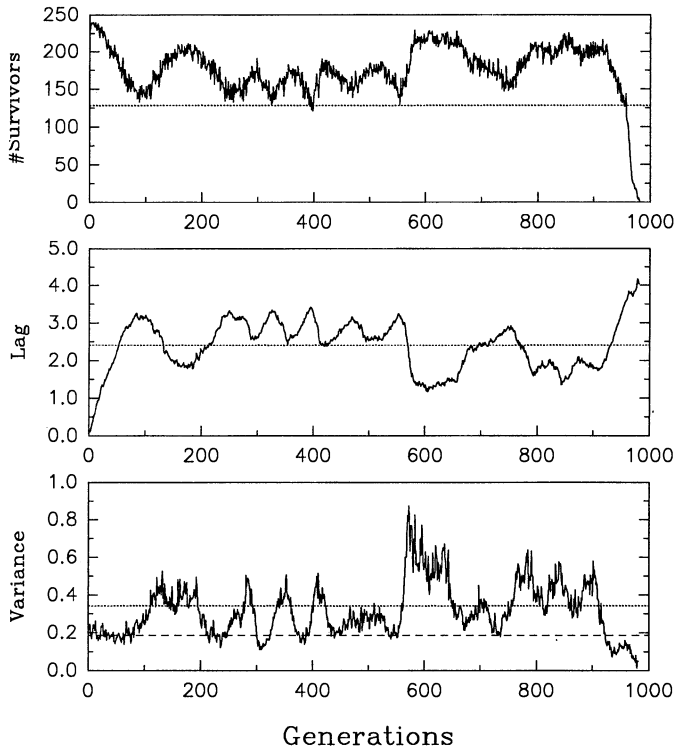


FIG. 5. Dynamics of the genetic variance $\sigma_{g,t}^2$ (lower panel), the lag of the mean phenotype $E[\bar{g}_t] - kt$ (middle panel), and the number of surviving offspring $B\bar{W}_t N_t$ (upper panel), for one particular run. The rate of environmental change is $k = 0.075$ which is near the critical rate of $k_c \approx 0.08$. The other parameters are $B = 2$, $\omega^2 = 9$, $\sigma_0^2 = 0$, $K = 128$. The dashed straight lines are (from top to bottom): the carrying capacity $K = 128$; the expected lag of the mean, $E[\bar{g}_t] - kt = 2.40$; and the neutral (dots) and SHC-expectation (dashes) (eqs. (15) and (14)) for the genetic variance. The average variance for this run is $\sigma_g^2 = 0.317$, compared to $\sigma_g^2 = 0.342$ from the neutral expectation, and $\sigma_g^2 = 0.184$ from the SHC-approximation. The time to extinction is 981 generations. For this parameter combination, the average time to extinction from 100 replicate runs is 449 generations; the average genetic variance is $\sigma_g^2 = 0.277$; and the average lag is 2.54.

even for large K . For $k = 0$ (constant stabilizing selection), (8b) is approximately correct (cf. also Bürger and Lande 1994). According to (8b), however, $V[\bar{g}]$ is independent of k . Our simulations show that this is not the case. As the rate of environmental change k increases, so does the variance of the mean phenotype, and it may be more than 10 times as large as the prediction. There are several reasons for the poor performance of the analytical approximation for $V[\bar{g}_t]$. For example, variability and autocorrelation of σ_g^2 have been neglected, and the derivation is based on a Gaussian assumption. Although our simulations show (see below) that the distribution of breeding values is approximately Gaussian on the average, temporal deviations from the Gaussian form do occur for any single population. Clearly, the fact that (7b) underestimates the variance of \bar{g} is one of the reasons our theory often predicts much longer extinction times than observations by simulations. We conclude that random excursions of the mean phenotype from its expectation are an important genetic determinant of risk to extinction for populations subject to environmental change.

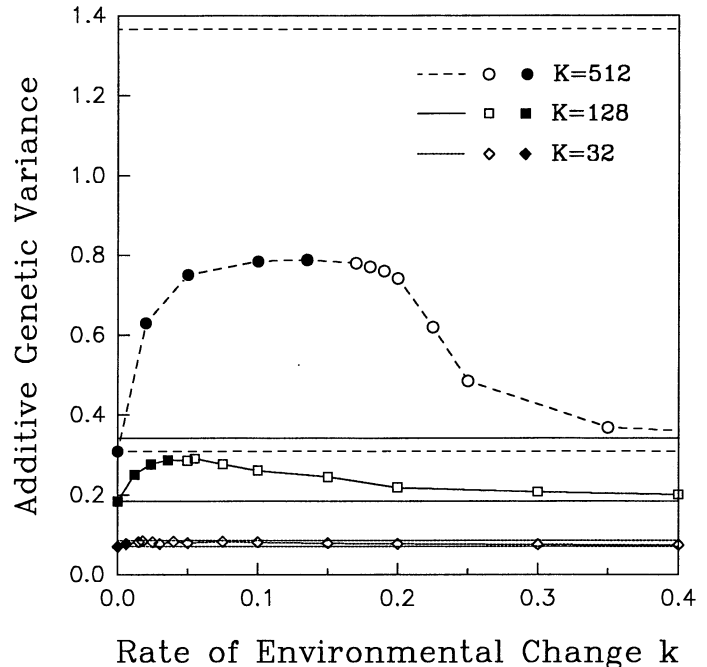


FIG. 6. The observed genetic variance as a function of the rate of environmental change, for three carrying capacities. For each K , the observed variance (symbols and connecting lines), as well as the neutral (15) and SHC-approximation (14) for the variance are shown (straight lines of the same kind as for corresponding data). Open symbols refer to k values where all populations became extinct. Filled symbols refer to k values where no population died out. Filled symbols are either averages over 5000 generations for 40 replicate runs, or averages over 25,000 generations for eight replicate runs.

Previous studies of directional selection have shown that the genetic variance in finite populations asymptotically tends to the neutral prediction (15) for truncation selection (Hill 1982), and for exponential directional selection (Bürger 1993). However, it appears to be difficult to obtain an accurate theoretical prediction for σ_g^2 in the present context. The Gaussian theory predicts a value for the genetic variance that is only slightly below the neutral prediction (15) unless K is much larger than in our simulations, and this prediction is unaffected by deviations of the mean from the optimum (Latter 1970; Lynch and Lande 1993). On the other hand, an extension to finite population size of the rare-alleles approximation of Barton and Turelli (1987) fails to produce a reasonable approximation in the present model of a continuously moving optimum, because the deviation of the mean phenotype from the optimum is too large (their assumption [7.7] being violated), and rare mutant alleles go to fixation during evolution.

We observed that the additive genetic variance increases from its initial mutation-selection-drift equilibrium value (14), as it responds to the moving optimum. Due to a combination of directional and stabilizing selection, however, the variance stays below the neutral prediction (15). Figure 6 displays the observed average genetic variance as a function of k for three different population sizes and moderately strong stabilizing selection. The open symbols represent values at which all populations became extinct, whereas the closed

symbols represent values where no extinction occurred in our simulations. For large k , the genetic variance remains at a level close to the SHC prediction because populations become extinct before the genetic variance can respond to directional selection.

The importance of the genetic variance for the extinction process is underscored by the high correlation (among replicate runs of the same set of parameters) between genetic variance and extinction time. Typical numerical values for this correlation range from 0.5 to 0.8, with a maximal observed value of 0.89. There appears to be little linkage disequilibrium generated, because the average genic variance is only a few percentage points higher than the average genetic variance. Since $\sigma_g^2 = 1$, heritabilities range from 0.08 ($K = 32$) to 0.45 ($K = 512$, $k = 0.15$).

Finally, we measured the skewness (the third central moment divided by σ_g^3) and kurtosis (the fourth central moment divided by σ_g^4) of the breeding values. The average skewness was always very slightly positive (typically 0.01 to 0.1), and the average kurtosis very near to three, indicating an almost perfect average Gaussian shape. The distribution of each single population, however, may deviate significantly from Gaussian at any particular time.

A Fluctuating Optimum

Here we assume that $k = 0$, so that all environmental change is due to random fluctuations of the optimum with variance σ_o^2 . In contrast to the case of a moving optimum where any population harboring little or no genetic variance is doomed to rapid extinction, for a fluctuating but otherwise constant optimum, genetic variability is not necessary for survival. In order to investigate the influence of genetics on population extinction for a fluctuating optimum, and to facilitate comparison with purely ecological theories of extinction due to demographic and environmental stochasticity, we performed additional simulations for monomorphic populations in which all individuals have a genotypic value of zero (fig. 7). (Formally, this is a special case of our model if we put $\mu = 0$, $\sigma_g^2 = 0$, $E[\bar{g}] = V[\bar{g}] = 0$.) Monomorphic populations (open symbols) survive longer than genetically variable populations, the difference being smaller for larger population sizes. The reason is that variable populations respond to fluctuations of the optimum, but with a time lag of one generation. On the average, this reduces their fitness in the subsequent generation, compared to a monomorphic population at $\bar{g} = 0$, because the optimum has a 50% chance of changing in the opposite direction to evolution in the preceding generation. In addition, phenotypic variance induces a load by reducing the expected growth rate (see eq. (9), and Lynch and Lande 1993).

Once the standard deviation σ_o of random fluctuations reaches the same order of magnitude as the width ω of the fitness function, any population is in danger of being extinguished suddenly, and genetics makes little difference. In this case, rare large shifts in the optimum occur that reduce the population number greatly.

Since there is a vast amount of literature on models of environmental stochasticity (Lewontin and Cohen 1969; Ludwig 1976; Turelli 1977; Leigh 1981; Tuljapurkar 1982; Lande

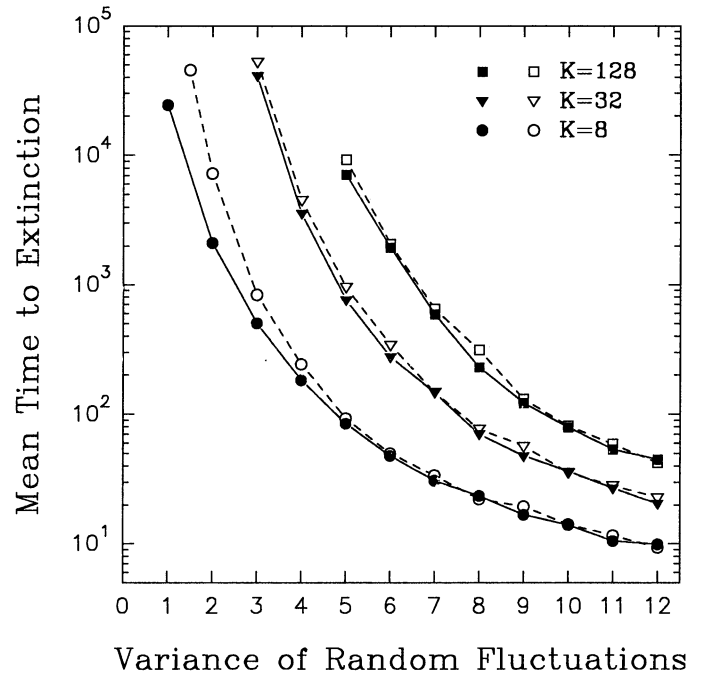


FIG. 7. Mean time to extinction as a function of the variance σ_o^2 of random fluctuations of an otherwise constant optimum ($k = 0$), for three carrying capacities. The other parameter values are $B = 2$, and $\omega^2 = 9$. The filled symbols are from simulations including genetics, whereas the open symbols are from simulations for a monomorphic population with genetic value equal to zero.

and Orzack 1988; Lande 1993), one might be optimistic and hope that these apply in the current context. However, this optimism is not justified. With $k = 0$, the quasi-deterministic approach predicts infinite extinction times for $\sigma_o^2 < B^2\omega^2 - V_s - \sigma_g^2 - V[\bar{g}]$ whereas our simulations show that extinction occurs rapidly for much smaller values of σ_o^2 . The reason is that the quasi-deterministic approach does not account for stochastic fluctuations in the growth rate, but incorporates only the (weak) influence of σ_o^2 on mean fitness. Additionally, our model includes demographic stochasticity generated by viability selection. The corresponding infinitesimal variance is easily calculated, and Leigh's (1981) diffusion model combining demographic and environmental stochasticity can be extended to the present situation. Still, this approach leads to overestimates of the mean extinction time by one or more orders of magnitude (results not shown). The reason is that the diffusion approximation is only accurate for long-run growth rates very near to zero, which is not the case for the parameters we investigated. In the case of pure demographic stochasticity, this was noticed by Gabriel and Bürger (1992). Other combined treatments of demographic and environmental stochasticity (cf. Wissel and Stöcker 1991, and refs. therein) do not apply here because they are based on branching processes, thus neglecting density dependence.

A Fluctuating and Moving Optimum

As noted above, temporal fluctuations of an otherwise stationary optimum may lead to a considerably increased risk of extinction. Figure 8 shows the combined effect of sto-

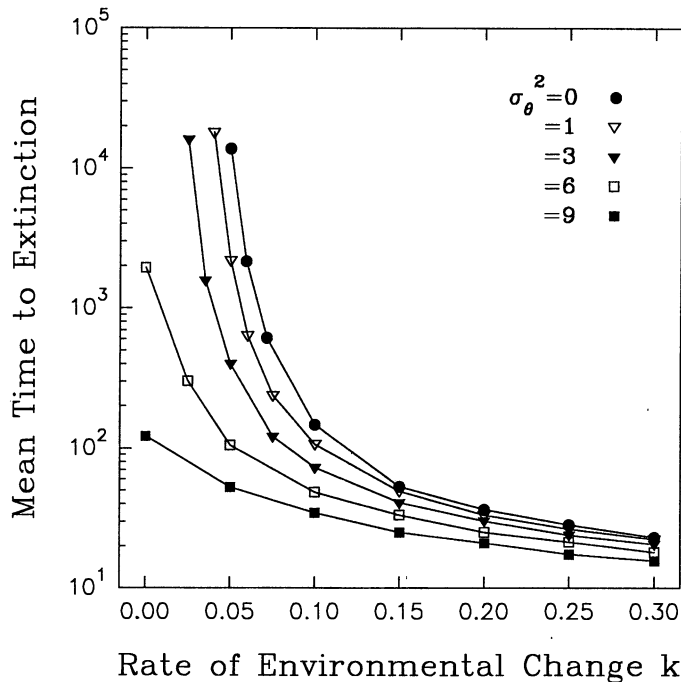


FIG. 8. Mean time to extinction as a function of the rate of environmental change, for five levels of temporal fluctuations in θ . The other parameters are $B = 2$; $K = 128$; and $\omega^2 = 9$.

chastic environmental change with a directional component. Populations that would be able to evolve and cope with a steadily changing environment may become extinct rapidly if random fluctuations of appreciable size occur. If the rate k of environmental change is already too high for a population to adapt, random fluctuations add little to the extinction risk.

In this general case, we are not in the position of presenting reasonably good analytical approximations. The quasi-deterministic approach fails because, among others, it neglects random variation in the growth rate R_t . The use of the long-run growth rate ρ_t instead of the λ_t leads to lower values of k_c and \bar{t}_e , but they are still considerable overestimates.

DISCUSSION

Although a substantial body of theory has been developed on the relationship of environmental change to extinction probability (Ludwig 1976; Leigh 1981; Tier and Hanson 1981; Goodman 1987; Lande 1993), all of these studies have focused on genetically monomorphic populations in a stochastically varying environment with no directional trend. Our primary concern, and that of Pease et al. (1989), Lynch et al. (1991), and Lynch and Lande (1993), is with the consequence of a long-term environmental trend, such as global warming. For a population lacking in genetic variation, there can be only one consequence of such environmental change—eventual extinction. Genetic variation replenished by recurrent polygenic mutation enables a population to adapt to a changing environment. No amount of genetic variation will enable a population to track the environmental optimum perfectly. However, if the rate of environmental change is sufficiently slow and the amount of genetic variance for the

selected trait is sufficiently high, the population mean phenotype settles into a quasi-steady-state lag behind the environmental optimum. The magnitude of this lag, relative to the width of the fitness function, determines the mean fitness of the population, which in turn determines the risk of extinction. Above a critical rate of environmental change, the lag load becomes so high that the population cannot replace itself, and rapid extinction becomes almost certain.

Finite populations exposed to stochastic events are doomed to eventual extinction. Nevertheless, there is a sharp boundary in the relationship between the rate of environmental change and mean extinction time, such that below a critical rate of change the population can track the environmental trend sufficiently closely to guarantee long-term survival. With the models that we have employed, this critical rate of change is typically on the order of 10% or less of a phenotypic standard deviation per generation. As noted above, for situations in which the rate of environmental change is sufficiently far below the critical rate, the mean phenotype is expected to settle into an evolutionary trajectory that lags behind the environmental optimum, but is otherwise parallel to it. Thus, the critical rate of environmental change is formally equivalent to the maximum sustainable rate of phenotypic evolution (Lynch and Lande 1993).

Our analyses seem to be the first to formally consider the joint role of environmental change and genetic and demographic stochasticity in the extinction process. As noted above, these factors interact in a synergistic way, often leading to much more rapid extinction than expected, based on the operation of single factors that have been the focus of most previous studies (cf. Goodman 1987; Lande 1993). This is most clearly illustrated for our results with rates of environmental change close to the extinction threshold—populations became extinct at rates of environmental change below the threshold predicted by the theory of Lynch and Lande (1993), which assumed a constant level of genetic variance. Genetic stochasticity resulting from several factors (random mutation and recombination, viability selection, random culling of excess progeny, and random sampling of gametes) leads to large temporal fluctuations in genetic variance. Periods of stochastic loss of genetic variation can be quite prolonged, due to the waiting time required for the replenishment of variation by mutation. During such bottlenecks, the mean phenotype can lag behind the optimum to such a high degree that extinction is almost certain, even though it would be unlikely if the genetic variance remained stable at its equilibrium expectation.

Viability selection was the only source of demographic stochasticity in our simulations, since we forced the sex ratio to be 1:1 and maintained a constant family size. When progeny numbers are treated as Poisson variables and sex ratios as binomial variables, dramatic declines in the mean extinction time are observed in small populations, even in the absence of environmental stochasticity (Gabriel and Bürger 1992), and when demographic stochasticity occurs in a population with genetic variance for fitness, the mean extinction time can drop by orders of magnitude (Gabriel et al. 1991).

The monogamous mating system that we employed, in combination with fixed family size, yields an effective population size that is in excess of the actual number of repro-

ducing adults. Thus, in addition to minimizing demographic stochasticity as a source of extinction, the simulations that we employed led to the maintenance of higher levels of genetic variance than would be expected in a randomly mating population. Preliminary simulations indicate that a highly kurtotic mutant distribution leads to somewhat lower extinction times than the Gaussian mutant distribution we have used here. The reason appears to be that under such a mutant distribution, a larger fraction of mutants is neutral while a few mutants have large effects, thus producing more genetic stochasticity. Taking all of these factors into consideration, it seems likely, for most organisms, that the critical rate of environmental change will be on the order of 1% or fewer phenotypic standard deviations per generation.

As noticed by Lynch and Lande (1993), even below the critical rate, because of functional and developmental constraints, no character can be expected to evolve directionally for an indefinite period of time. However, based on long-term selection experiments with small populations, evolution of 10 or more phenotypic standard deviations is possible. If the critical rate is on the order of 1% of a phenotypic standard deviation, this rate of evolution could be sustained for several hundreds or even thousands of generations, before functional or pleiotropic constraints are encountered.

Huey and Kingsolver (1993) applied the model of Lynch and Lande (1993) to the evolution of thermal sensitivity. On the basis of this model, they investigated how the shapes of thermal performance curves affect the evolutionary responses of a population to a gradual, directional climate change. Their theoretical predictions depend crucially on the relationship between the genetic variation in optimal temperature and the width of the fitness function (performance breadth). Under the assumption that the genetic variance is independent of the width of the fitness function, Huey and Kingsolver suggested that there might be an intermediate width that maximizes the critical rate of environmental change (and hence maximizes the time to extinction). They argued that, by reducing the intensity of selection, too wide a fitness function leads to a high lag load, whereas an excessively narrow fitness function reduces the lag, but nevertheless induces a very high load. On the other hand, on the basis of a Gaussian approximation (cf. Lynch and Lande 1993), they found that the critical rate of change increases as the width of the fitness function increases. Our simulations, allowing the genetic variance to evolve in response to selection, show that there indeed is an intermediate width of the fitness function that maximizes the mean extinction time in a changing environment, unless the environment changes too fast. This suggests that in a slowly, but steadily, changing environment, broad generalists and narrow specialists will be most vulnerable to extinction.

Several technical issues in evaluating the influence of environmental change on the risk of extinction remain unsolved. First, although we have been successful in obtaining an analytical approximation to the mean extinction time for situations in which extinction is likely to occur within time periods of 100 generations or so, the theory is not yet adequate for describing the situation when the rate of environmental change is near or below the critical rate. Second, even for cases in which we are able to predict the mean extinction

time analytically, no theory has been forthcoming for the probability distribution of extinction time. Typically, our results show a strongly skewed distribution, with the mode being significantly below the mean. Since the coefficient of variation of extinction time depends strongly on the genetic and ecological parameters, it is clear that the mean extinction time alone does not provide sufficient information to describe the risk of a population to extinction.

ACKNOWLEDGMENTS

We thank R. Lande for helpful discussion and R. Lande, J. Kingsolver, and a reviewer for comments on the manuscript. The work has been supported by a research exchange grant from the Max Kade Foundation to R.B., and by NSF grants BSR 8911038 and BSR 9024977, and PHS grant GM36827 to M.L. Numerical simulations were performed on the IBM ES/9021-720 mainframe of the EDV-Zentrum der Universität Wien as part of the IBM Supercomputing Program for Europe. We are grateful for generous access to computing time.

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