WHEN DOES EVOLUTION BY NATURAL SELECTION PREVENT EXTINCTION?

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Understanding population responses to novel environments is a central concern of both evolutionary biology and ecology (Maynard Smith 1989; Bradshaw 1991; Hoffman and Parsons 1991; Peters and Lovejoy 1992; Kareiva et al. 1993). Populations subject to substantial environmental stress, such as occurs during colonization attempts, human-mediated introductions or reintroductions, or global climatic change, may face a risk of extinction. There are many examples of such extinctions, but many examples are known in which populations have evolved sufficiently to persist in changed environments, such as cases of evolved resistance to pesticides or heavy metal toxins (e.g., Bradshaw 1991). An important problem for evolutionary biologists is thus to characterize those combinations of genetic and demographic conditions likely to result in persistence versus those expected to lead to extinction in a changed environment.

Theoretical work has characterized circumstances in which populations have sufficient genetic capacity to avoid extinction by adapting with sufficient speed to a continuously changing environment (Pease et al. 1989; Lynch et al. 1991; Lynch and Lande 1993; Bürger and Lynch 1994). Here we use simple models to highlight an additional risk faced even by populations genetically capable of evolving sufficiently to persist in environments that remain constant following a single, initial abrupt change. Namely, as a population adapts to a novel environment, its density may fall below a critically low level for a period of time, during which the population is highly vulnerable to extinction by demographic stochasticity. If this occurs, the population is likely to vanish before it can be rescued by evolution.

To examine this problem, we coupled models of population dynamics and of evolution by natural selection to identify conditions for which evolution succeeds—or fails—to rescue a closed population from extinction following abrupt environmental change. The models considered here cover extremes in both genetics (one-locus and polygenic models) and population growth (discrete and continuous-time models). These models lead to a similar conclusion: even populations with the genetic wherewithal to potentially persist in a novel environment may often fail to do so. Moreover, our analyses help to quantitatively characterize situations in which evolution by natural selection can effectively rescue a population from impending extinction. We suspect the qual-

itative properties of our results may be general features of evolutionary dynamics in novel environments.

MODELS AND ANALYSIS

Models of demographic stochasticity (e.g., Goodman 1987; Lande 1993) have identified densities below which populations risk rapid extinction, even in constant environments. Closed populations whose per-capita finite growth rates remain below unity will deterministically reach such critically low densities (fig. 1A). Evolution by natural selection can affect population persistence by influencing population mean fitness, here equated with mean per-capita growth rate (Crow and Kimura 1970). Fisher's fundamental theorem (Fisher 1958; Frank and Slatkin 1992) suggests, roughly, that natural selection increases population mean fitness, given heritable variation for fitness. In what circumstances can evolution increase a declining population's growth rate sufficiently rapidly to prevent the population from deterministically reaching a given critical low density (as for the population with growth trajectory *a* in fig. 1B)?

A Simple Two-Step Model

The following elementary model captures the essence of this process. Imagine a population that has experienced an abrupt change in its environment (such as a group founding an isolated colony in a novel habitat, or a closed island population that has experienced a rapid, steplike change in its local environment) that places it at risk of deterministic extinction. That is, immediately following the change in its environment at time $t = 0$, we assume the population has mean absolute fitness $\bar{W}_0 < 1$ and density N_0. Assuming nonoverlapping generations, the deterministic dynamics of population size in generation t are described by

$$N_t = \bar{W}_{t-1} N_{t-1}, \tag{1}$$

where $\bar{W}_t$ is the absolute mean fitness (finite per-capita growth rate) in generation t.

Now suppose there is a critical density, denoted N_c, below which the population is highly susceptible to rapid extinction by demographic stochasticity. The notion of a critical density is used here as a heuristic device to examine the influence of evolution on extinction (see the Discussion below). N_c is basically a "rule-of-thumb" density, above which it is rea-
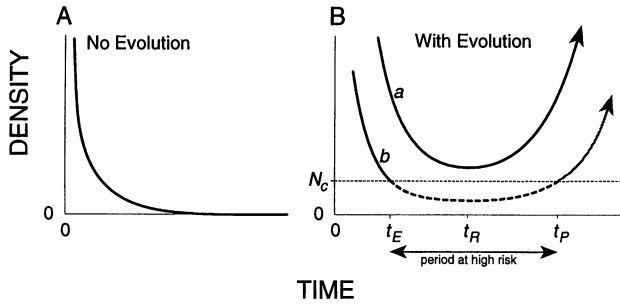
FIG. 1. Population growth in a novel environment. Without evolution (A), a maladapted population inevitably declines to extinction. With evolution (B), an initially maladapted population may eventually grow. Trajectory a: the population does not encounter a high risk of extinction, because it evolves growth quickly enough to remain above critically low densities. Trajectory b: the population is highly vulnerable to extinction by demographic stochasticity because, at time t_E, it declines to critically low densities (below N_c) before it can evolve growth (at time t_R). Provided it continues to avoid extinction, the population will, at time t_P, grow above critically low densities, ensuring its deterministic persistence. The population is highly vulnerable to extinction for a period of duration $t_P - t_E$.
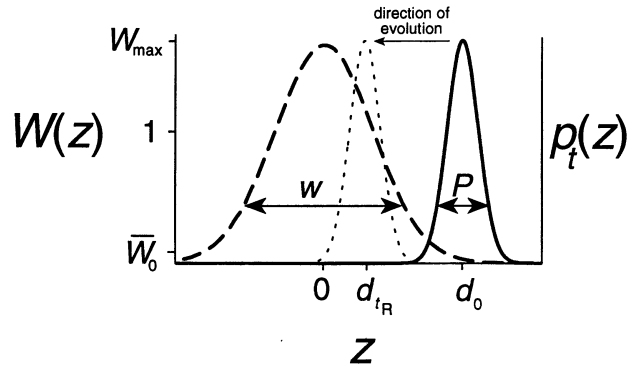

FIG. 2. Graphic portrayal of the basic elements of an evolutionary quantitative-genetics model. A quantitative trait (z) in a closed population at generation t is distributed according to a normal density function ($p_t[z]$) with mean d_t and variance P (solid curve). Just after an abrupt environmental change, the mean phenotype is d_0. Individual fitness (dashed curve) follows a Gaussian function ($W[z]$), with width w, and optimal phenotype at $z = 0$. The initial growth rate (at $d = d_0$) is $\bar{W}_0 < 1$. Evolution moves the mean phenotype toward the fitness optimum, and when $d_t < d_{t_R}$ (i.e., the mean phenotype lies to the left of the dotted distribution's mean), the population will grow, because $\bar{W}_t > 1$ for $t > t_R$. If the time, t_R, required to move from d_0 to d_{t_R} is too great, the population risks extinction because of its declining numbers.

sonable to ignore demographic stochasticity. Theoretical models often suggest N_c lies in the range 10–100 (MacArthur and Wilson 1967; Lande 1993).

Assume the new environment remains constant. Then, without evolution, $\bar{W}_t = \bar{W}_0$ for every t, and the population reaches N_c in

$$t_E = (\ln N_c - \ln N_0)/\ln \bar{W}_0 \qquad (2)$$

generations. This expression also provides a reasonably accurate approximation of the mean time to extinction in a declining population, given demographic stochasticity (Lande 1993, eq. 5c).

Of course, absolute mean fitness itself may change as the population evolves. If, say, selection were to increase mean fitness by a fixed amount δ each generation, the population would require $t_R = (1 - \bar{W}_0)/\delta$ generations to evolve a per-capita growth rate that exceeds unity (i.e., $\bar{W}_t > 1$ for $t > t_R$; see fig. 1B), allowing the population to rebound from its initial decline. If $t_R < t_E$, persistence is likely; if $t_E < t_R$, the population may face a period of dramatically increased extinction risk because it is below N_c. This simple model shows that the problem of population persistence in a novel environment can be viewed as a race between two processes, one demographic, another evolutionary (as suggested by Maynard Smith 1989), operating at different characteristic time scales: t_E and t_R.

A Discrete-Time, Quantitative-Genetic Model

In more realistic models, mean fitness will not increase at a constant per generation rate. Nevertheless, the overall dynamics of the system can still be viewed as a race between demographic and evolutionary processes. For instance, consider the evolution of an ecologically important quantitative trait, z, with polygenic autosomal inheritance (Lande 1976) (e.g., a character like metabolic rate that governs environ-

mental influences on fitness). Suppose the population has just colonized a new habitat or experienced abrupt in situ environmental change, such that z is subject to selection in its altered surroundings. (We neglect mutation and drift.)

In the new environment, assumed constant, the optimal phenotype (measured on an appropriate scale) has absolute fitness W_{max} at $z = 0$. We assume absolute fitness is described by a Gaussian function with width w: $W(z) = W_{max} \exp[-z^2/(2w)]$ (fig. 2). In generation t following the change in environment, the phenotype z follows a normal distribution ($p_t[z]$), with variance P and mean d_t (our notation emphasizes the distance of the population mean from the optimum at $z = 0$; see fig. 2). The absolute mean fitness in generation t is $\bar{W}_t = \int p_t(z)W(z)\, dz$.

We assume discrete, nonoverlapping generations and population growth described by (1), so that

$$N_t = N_0 \prod_{i=0}^{t-1} \bar{W}_i. \qquad (3)$$

By comparison, many models of discrete population growth take the form

$$N_{t+1} = N_t \bar{W}_t g_t(N_t),$$

where $0 \le g_t(N) \le 1$ expresses density dependence depressing population growth below the maximum possible in generation t, $\bar{W}_t$. In using (1), we assume that the absolute population mean fitness ($\bar{W}_t$) is a function of the single phenotypic variable (z) and is independent of N_t; that is, the evolutionary dynamics of z and, consequently, $\bar{W}_t$ are density independent. Moreover, we assume that $g \equiv 1$. Although this is probably a reasonable approximation in particular cases (such as for colonizing propagules), in general, setting $g \equiv 1$ establishes an upper bound to population decline given that

$$N_t = N_0 \prod_{i=0}^{t-1} \bar{W}_i g_i(N_i) \leq N_0 \prod_{i=0}^{t-1} \bar{W}_i.$$

Thus, the density-independent population dynamics we use in our analysis (eq. 3) provide a kind of best-case scenario for deterministic population persistence.

By standard results (Lande 1976; Bulmer 1985; Falconer 1989), the distance of the mean phenotype from the optimum, d_t, changes each generation by

$$\Delta d_t = -h^2 \, d_t P/(P + w), \tag{4}$$

where h^2 is the heritability of z. Assuming for simplicity fixed P and h^2, the mean phenotype approaches the new optimum geometrically:

$$d_t = k^t d_0, \tag{5}$$

where $k = [w + (1 - h^2)P]/(w + P)$, and d_0 is the initial distance of the population mean from the optimal phenotype. The quantity k determines the evolutionary inertia of the character; $0 \leq k \leq 1$. If $k = 1$, there is no evolution and, for given w and P, if $k = w/(w + P)$, evolutionary equilibrium is approached at the maximum speed possible. The dynamics of mean fitness are described by

$$\bar{W}_t = \hat{W} \exp[-d_t^2/2(P + w)], \tag{6}$$

where $\hat{W} = W_{max}\sqrt{w/(P + w)}$ is the growth rate of a population with the mean phenotype at its optimum ($d = 0$).

Assume $\bar{W}_0 < 1$, so that without evolution, extinction is inevitable. In this model, natural selection increases mean fitness (Lande 1976). Were a population to achieve its evolutionary equilibrium in this environment, its growth rate would equal its mean fitness maximum, $\hat{W}$ (which is less than W_{max} because of the continual generation of suboptimal phenotypes assumed in our quantitative-genetics formulation). Even with evolution, if $\hat{W}$ is less than one, persistence is impossible in the novel environment, because a population with a maximal mean fitness of less than one certainly declines to extinction (Lynch et al. 1991), as in the case of no evolution (fig. 1A). In contrast, if $\hat{W} > 1$, a population can potentially persist (fig. 1B). There are two cases to consider: (1) extinction in the novel environment is likely to be avoided (i.e., N_t is always above N_c), because $\bar{W}_t$ increases sufficiently fast (trajectory a in fig. 1B); (2) although a growth rate exceeding unity is evolutionarily feasible, the population nonetheless is highly vulnerable to extinction, because its size dips below N_c for a period of time (trajectory b in fig. 1B). In the latter case, population size declines, passing below N_c at time t_E, until mean fitness exceeds one after a time t_R. The population then grows but continues to remain below N_c until time t_P.

If a population's density is initially below N_c, then $t_E = 0$. If $N_0 > N_c$, then using equations (3)–(6) and some algebraic manipulations, we derived an implicit expression for the times, t_E and t_P, at which $N_t = N_c$. These times are the roots t of

$$t \log \hat{W} - \frac{\beta_0}{2}\left(\frac{1 - k^{2t}}{1 - k^2}\right) = \log \nu_0, \tag{7}$$

where $\beta_0 = d_0^2/(w + P)$ (measuring the degree of initial maladaptation), and $\nu_0 = N_c/N_0$ (indicating how close the initial population is to its extinction vulnerability threshold).
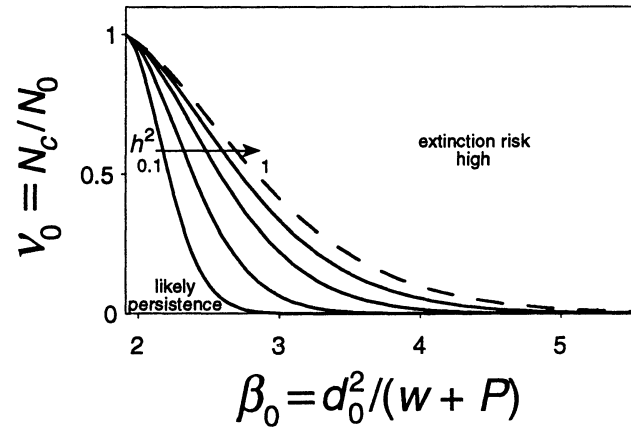

$$\beta_0 = d_0^2/(w + P)$$

FIG. 3. Combinations of initial population densities and degrees of initial maladaptation leading to likely population persistence or high extinction risk for five levels of heritability (solid curves: h^2 = 0.1, 0.25, 0.5, 0.75; dashed curve: h^2 = 1). For a population evolving according to the quantitative-genetic model described in the text and figure 2, the graph indicates those initial population densities and initial phenotypic means for which it either remains above or falls below N_c. The initial population size (N_0) is scaled inversely to N_c (i.e., small values of ν_0 indicate large initial densities relative to the critical density). The initial degree of maladaptation (β_0) is measured as the squared initial distance (d_0^2) of the population mean phenotype from the fitness optimum scaled to the width (w) of Gaussian stabilizing selection and phenotypic variance (P) (see fig. 2; $\hat{W}$ = 2.59; P = 0.1w). For each level of heritability, populations with ν_0 and β_0 below the curve persist deterministically, because they are bounded above N_c by sufficiently rapid evolution; those above the curve eventually decline below N_c and become highly vulnerable to rapid extinction by demographic stochasticity.

Numerical analysis of equation (7) reveals either zero or two biologically meaningful (i.e., real, nonnegative) roots for each combination of parameters. Cases with no roots correspond to trajectory a in figure 1B, and those with two roots correspond to trajectory b.

Figure 3 shows those combinations of initial population densities and degrees of initial maladaptation that lead to likely persistence, versus high extinction risk (case [1] vs. case [2]) for five different heritabilities (h^2 = 0.1, 0.25, 0.5, 0.75, 1). Populations which are initially above N_c (corresponding to $\nu_0 = N_c/N_0 < 1$) and experience a mild environmental change (β_0 small) will certainly be rescued by evolution (i.e., N_t remains above N_c) over a wide range of initial population densities and heritabilities. In contrast, with more drastic environmental changes (β_0 large), only populations greatly exceeding their threshold densities ($\nu_0 \ll 1$) with high heritabilities are likely to be rescued by natural selection. At low heritabilities and intermediate levels of environmental change, the range of initial population sizes consistent with N staying always above N_c drops off in an almost step-like fashion.

Figure 4 illustrates the dependence of the time t_E at which a population first reaches N_c on its initial degree of maladaptation (β_0). Populations that are sufficiently mildly maladapted (β_0 less than a critical level, β^*; see fig. 3) never fall below N_c. For populations that are initially more severely maladapted ($\beta_0 > \beta^*$), t_E declines with increasing β_0. The
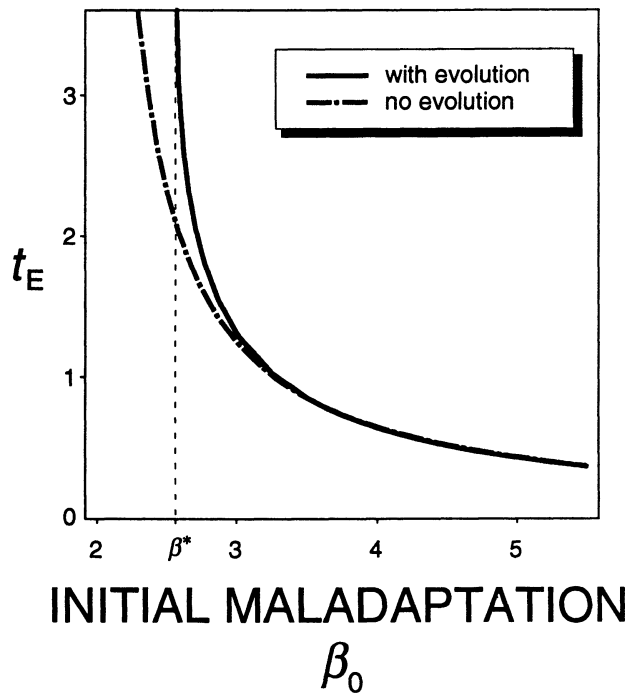
FIG. 4. The time t_E a population will first reach the critical density as a function of its initial degree of maladaptation for the quantitative-genetic model ($\hat{W} = 2.59$, $P = 0.1w$, $h^2 = 0.5$; $N_0 = 2N_c \leftrightarrow v_0 = 1/2$.). The solid curve shows the smaller roots of equation (7) when they exist ($\beta_0 > \beta^*$). The dot-dashed curve indicates analogous times for the case of no evolution (eq. 2).

dependence of t_E on β_0 is strong for populations that are not severely affected, but is weak for highly maladapted populations. For comparison, the relation between t_E and β_0 in the extreme case of no evolution ($\bar{W}_t = \bar{W}_0$ for all t; see eq. 2) is shown by the dot-dashed curve. Evidently, the major effect of evolution is to keep mildly maladapted populations from ever reaching critically low levels. However, for populations bound to experience critically low densities (i.e., $\beta_0 > \beta^*$), evolution causes almost no delay in the time such levels are first reached.

The dependence of t_E on initial population density, scaled as $v_0 = N_c/N_0$, is qualitatively similar to the dependence of t_E on β_0 shown in figure 4 (see also fig. 5B, solid curve). Populations that are initially sufficiently large (v_0 less than a critical number, v^*) will never reach critically low densities. For populations initially closer in size to $N_c(v^* < v_0 < 1)$, t_E decreases with decreasing initial population size (increasing v_0) but is essentially independent of N_0 for initial sizes close to (or, obviously, below) N_c. There is also a near-threshold effect of evolution on t_E: a population's initial size tends to be such that reaching critical densities is avoided entirely, or they are reached almost as quickly as in the absence of evolution.

If $\hat{W}$ is sufficiently large, for fixed values of the other parameters and initial conditions there is no feasible solution for equation (7), implying the population never declines below N_c. This suggests that populations with relatively high

potential growth rates in a novel environment should be more able to escape extinction via evolution, compared to populations with lower potential growth rates.

We have assumed populations below N_c are highly vulnerable to extinction resulting from demographic stochasticity. However, provided they manage to avoid extinction, such populations continue to adapt and, eventually, will grow again (if $\hat{W} > 1$). The time t_R needed for a population to evolutionarily recover from a demographic decline (defined as the first time at which $\bar{W}_t \geq 1$) can be shown from equations (4)–(6) to satisfy

$$t_R = [\log \log \hat{W} - \log(\beta_0/2)]/\log k^2. \qquad (8)$$

This shows that t_R increases logarithmically with the degree of initial maladaptation β_0 but is independent of the initial population density (v_0). That is, an initially more severely maladapted population requires more time than a mildly maladapted population to evolve the sufficiently high mean fitness that allows it to increase in density.

Even a growing population that is below its critical density faces a high risk of extinction. However, provided the population continues to avoid extinction, at some point its density will grow above N_c, after which time the population is no longer at a significant risk of extinction owing to demographic stochasticity. For parameter combinations that place a population at high extinction risk, the first time t_P that a population's density could climb above N_c—so that its chances of persistence are substantially increased—is the larger of the (two) roots of equation (7).

The difference, $t_P - t_E$, between the first and last times a population would encounter critically low densities defines the period at which the population will be at high risk of extinction owing to demographic stochasticity (see fig. 1B). The longer a population is below N_c, and the smaller its abundance, the more likely it is to become extinct. To the extent that population sizes below N_c have similarly high probabilities of extinction, a population's risk of rapid extinction increases with the period ($t_P - t_E$) during which its size is deterministically below N_c. The dependence of this period on initial maladaptation or initial population size is shown in figure 5. For larger initial degrees of maladaptation, the duration of time at risk grows linearly with β_0 (fig. 5A). In contrast, the period at risk is relatively independent of initial density for initial densities near N_c (v_0 closer to 1; fig. 5B).

Relations (7) and (8) show that evolutionary and demographic dynamics of this model depend essentially on four quantities, two of which characterize a population's capacity for evolution and maximal growth in the novel habitat (k and $\hat{W}$), and two measure its initial degree of maladaptation and density (β_0 and v_0). Of these, $\hat{W}$ is probably the most difficult to determine empirically, because it is the long-term growth rate of a population that is initially in decline and, thus, most vulnerable to rapid extinction. However, both (7) and (8) can be rewritten, using the substitution $\hat{W} = \bar{W}_0 \exp[\beta_0/2]$ (see eq. 6), in terms of the rate of initial population decline in the novel environment ($\bar{W}_0$), a more readily observable quantity.

A Continuous-Time, One-Locus Model

To determine the sensitivity of the results in the previous section to the particular form of model (discrete-time, quan-
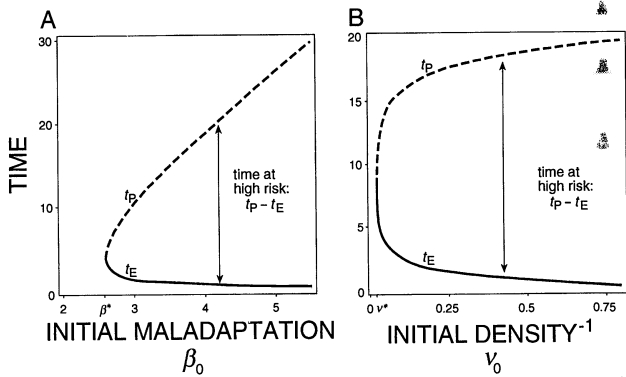
FIG. 5. The period at high risk of extinction as a function of initial maladaptation (A), or initial density (B), for the quantitative-genetic model. Parameters are as in figure 4 (graph A: $v_0 = 1/2$; graph B: $\beta_0 = 4$). Solid curves show t_E (first risk of extinction using the heuristic criterion $N < N_c$; fig. 4) and dashed curves show t_P (last risk of extinction, i.e., last time when $N < N_c$; larger roots of eq. 7) as functions of β_0 or v_0. For each value of β_0 or v_0, the period of high extinction risk is the distance between corresponding points on the upper and lower curves: $t_P - t_E$. Populations with mild degrees of initial maladaptation ($\beta_0 < \beta^*$) or large initial densities ($v_0 < v^*$) never fall below N_c, thereby avoiding high extinction risks.

titative genetic), we analyzed a substantially different model: a diploid, diallelic, one-locus genetic model with continuous selection and density-independent population growth (Crow and Kimura 1970; Nagylaki and Crow 1974). Here a population's infinitesimal per-capita growth rate is determined by its mean Malthusian fitness $\bar{m}_t$, which itself depends on the frequencies p_t and q_t of alleles A_1 and A_2 at time t. Assuming the conditions for Hardy-Weinberg proportions hold (Nagylaki and Crow 1974), $\bar{m}_t = p_t^2 m_{11} + 2p_t q_t m_{12} + q_t^2 m_{22}$, where m_{ij} is the Malthusian fitness of genotype $A_i A_j$ and $m_{21} = m_{12}$ (Crow and Kimura 1970; Nagylaki and Crow 1974). To focus on cases in which evolution can potentially save a declining population from extinction (fig. 1B), we assumed that in the novel environment $m_{11} = m_{max} > 0$ and $m_{22} = m_{max} - s$, where $s \geq m_{max}$. In addition, we assumed heterozygote fitness (m_{12}) is intermediate to the two homozygote fitnesses, thus, the initial frequency of A_2, q_0, gauges a population's initial degree of maladaptation (analogous to β_0).

Under these conditions, we combined standard results (Crow and Kimura 1970, pp. 191–193) with the population growth equation, $dN/dt \approx \bar{m}N$, to derive the times t_E, t_R, and t_P. In the case of no dominance ($m_{12} = m_{max} - s/2$), the first time a population encounters critically low densities, t_E, and the last time, t_P, are (when they exist) the smaller and larger nonnegative roots of

$$t[m_{max} - s] + 2 \log\{q_0 + [1 - q_0]\exp[st/2]\} = \log v_0, (9)$$

where $v_0 = N_c/N_0$ as above. Here the time t_R needed to evolve $\bar{m} \geq 0$ so that the population can grow is

$$t_R = 2\{\log[(s/m_{max}) - 1] + \log[q_0/(1 - q_0)]\}/s. (10)$$

The dependencies of the time required to reach N_c, t_E, and the period at risk, $t_P - t_E$, on the initial degree of maladaptation, q_0, are shown in figure 6.
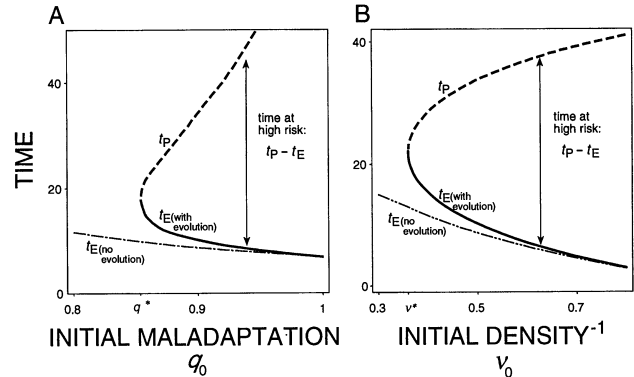

FIG. 6. The period at high risk of extinction as a function of initial maladaptation (A), or initial density^{-1} (B), for the one-locus model with no dominance ($m_{max} = 0.1$, $s = 0.2$; graph A: $v_0 = 1/2$; graph B: $q_0 = 0.9$). Solid curves show t_E (first risk of extinction, i.e., first time when $N < N_c$; smaller roots of eq. 9), and dashed curves show t_P (last risk of extinction, i.e., last time when $N < N_c$; larger roots of eq. 9) as functions of q_0 (initial frequency of an allele with deleterious effects in the new environment) or v_0. For each value of q_0 or v_0, the period of extinction risk is the distance between corresponding points on the upper and lower curves: $t_P - t_E$. Populations with sufficiently small frequencies of the deleterious allele ($q_0 < q^*$) or large enough initial densities ($v_0 < v^*$) avoid high extinction risk. Dot-dashed curves represent times at first risk of extinction (t_E) as a function of q_0 or of v_0 without evolution.

This one-locus, continuous-time model shares the qualitative features of the discrete-time, quantitative genetics model described above (compare figs. 5 and 6). Populations that are initially mildly maladapted ($q_0 < q^*$) or sufficiently large ($v_0 < v^*$) will never reach critically low densities. Populations that are initially more severely maladapted ($q_0 > q^*$) or smaller ($v_0 > v^*$) will be highly vulnerable to extinction. For such populations, the time when the critical density is first reached, t_E, decreases with increasing q_0 and v_0 (fig. 6, solid curves). Comparing these times to those in the case of no evolution ($\bar{m}_t \equiv \bar{m}_0$; dot-dashed curves in fig. 6), it is apparent that the major effect of evolution is to prevent a population from deterministically reaching critically low densities altogether. The time t_R at which population size would begin to grow (given extinction is avoided) and the period at high risk, $t_P - t_E$, both increase with q_0 and v_0. Similar qualitative results hold for clonal, haploid, and gametic diploid selection, which are all mathematically similar to the case of no dominance described above (Crow and Kimura 1970; Nagylaki and Crow 1974).

DISCUSSION

Our analyses reveal what we suspect are general features of the interplay between evolution and demography in novel environments. In particular, our findings indicate that only large populations that are initially not too severely maladapted might be expected to escape extinction resulting from demographic stochasticity. Populations that are initially more severely maladapted or initially small will reach critically low sizes sooner, and—should they happen to avoid immediate extinction—remain at dangerously low densities longer than larger, less severely affected populations. Only large or

mildly affected populations are expected to endure in the face of large environmental change. However, even large initial population sizes are no buffer against especially large changes. Moreover, unless colonizers are already well-adapted to the novel habitats they encounter, only colonizing groups (including deliberately introduced propagules) of large size or large ultimate maximal growth rates can be expected to flourish in exotic environments. This suggests a potential explanation for conservatism in species niches over evolutionary time (Holt and Gomulkiewicz unpubl. data).

These intuitively reasonable conclusions could be reached using verbal arguments. The models presented here allow the sharpening of this intuition. For instance, in the quantitative-genetics model, there is a near-linear relationship between the period at high risk of extinction and a quantitative measure of initial maladaptation (fig. 5A), and a step-like relationship between the range of initial densities consistent with likely persistence and the same measure of maladaptation (fig. 3). This latter property is consistent with data, from human-mediated species introductions, on the relation between propagule size and establishment success (e.g., Pimm 1991). Our analyses also reveal unanticipated qualitative features, including that evolution does little to slow the approach to critically low densities of populations destined to reach such densities (figs. 4, 6).

Lenski and Bennett's (1993) experimental results on the evolution of thermal tolerance in *Escherichia coli* are consistent with our theoretical expectations. This is a species with potentially large maximal growth rates and thus would seem to have a high chance of being rescued by evolution, compared with most other species. Yet even in this case, most populations failed to evolve sufficiently to persist in thermal environments outside the ancestral population's "thermal niche" (those temperatures at which chemostat populations can be maintained indefinitely under serial dilution).

Many published tables show that there are species with large maximal growth rates in environments to which they are well-adapted (e.g., Blueweiss et al. 1979). However, growth rate is a joint property of phenotype and environment. Species near the edges of their geographic range, or, more broadly, the limits of their ecological niche, tend to have low growth rates. Thus, our results should pertain to some populations in nearly all species. Furthermore, our models suggest that species that never have large maximal growth rates (e.g., resulting from large body size, specialized requirements, etc.) should be particularly vulnerable to extinction in changed environments.

It is difficult to relate our findings to most empirical and experimental studies of populations' rates of evolutionary progress under selection. The reason is simple. Empiricists are interested in studying responses to selection, which of course cannot be observed in populations that become extinct. Great effort is often expended in setting up conditions that ensure populations will persist. However, the rates of progress under selection appropriate for questions of evolutionary rescue we have addressed are those specifically associated with environments in which populations are prone to extinction.

The simple models presented above ignore a number of potentially important evolutionary processes. Still, we be-

lieve our results place upper bounds on the chances of population persistence, because other evolutionary forces tend to either increase maladaptation (e.g., most mutations; Houle et al. 1992) or reduce genetic variance (e.g., drift) and therefore slow a population's evolutionary response to a changed environment. Demographically, our assumption of density independence ensures, as explained above, a kind of maximal scope for deterministic population persistence.

An important limitation of the above models is that we assumed closed populations. Recurrent migration into an open population could conceivably either foster or hamper evolutionary rescue by selection. Recurrent migration rescues a population demographically, for if migrants appear in each generation, the population never actually becomes extinct (this implicitly assumes a source-sink structure; Holt 1993). These migrants, moreover, could provide an infusion of genetic variation upon which local selection can act, possibly allowing a sink population to evolve into a source. However, immigrants will, in general, be maladapted to the local environment, and gene flow could thus compromise the effects of local selection (e.g., Wright 1931). Evaluating the relative magnitudes of these opposing effects is a challenging task for future work. Still, our models suggest that the reciprocal of the time a population would first reach critically low densities ($1/t_E$) may provide a rough guide for the frequency of migration episodes required for a population to persist because of regular immigration or introductions. The results above should apply to combined population and evolutionary dynamics between such episodes.

Introducing a critical density below which a population is at a significantly increased risk of rapid extinction, as was done here, should be viewed as a heuristic approximation to a full analysis of extinction risk in a changed environment. Such a full analysis would portray population and evolutionary dynamics with genotypically explicit stochastic birth-death models, coupling standard approaches to assessing extinction risk in genetically homogeneous populations (Gabriel and Bürger 1992; Lande 1993; Mangel and Tier 1993) with population-genetic models for evolution in finite populations (Wright 1931; Fisher 1958; Moran 1958; Lande 1976). The desired result would be a frequency distribution for times to extinction in evolving populations, taking into account how the probability of extinction increases as mean effective population size decreases, and variance in a fluctuating environment increases. The parameters of this distribution, we surmise, will include initial population size and a measure of the initial degree of maladaptation, as did the above models.

The concept of a critical density is a broadly useful heuristic device for dealing with several distinct hazards associated with low population size. Although we invoked demographic stochasticity to motivate N_c, it should be noted that other biological factors (such as inbreeding depression or Allee effects) can also lead to sharply increased extinction risks at low densities.

Our results complement work on evolutionary rescue in continuously changing environments (Pease et al. 1989; Lynch et al. 1991; Lynch and Lande 1993; Bürger and Lynch 1995) by highlighting the demographic risks faced even by populations with the genetic capacity to evolve fitness suf-

ficient for deterministic persistence in a new environment. Our findings suggest, alas, that only mildly affected populations at high natural densities can reasonably be expected to be rescued by evolution in novel environments.

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Corresponding Editor: G. Vermeij

DECEIT POLLINATION AND SELECTION ON FEMALE FLOWER SIZE IN *BEGONIA INVOLUCRATA*: AN EXPERIMENTAL APPROACH

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For two centuries, biologists have recognized that the extraordinary diversity of floral traits, such as size, shape, color, and odor, is a consequence of the ecological and evolutionary interactions between plants and their pollinators (Sprengel 1793; Darwin 1877; Müller 1883; Leppik 1957; van der Pijl 1961; Baker 1963; Grant and Grant 1965). Natural selection