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Demographic and Genetic Constraints on Evolution

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ABSTRACT: Populations unable to evolve to selectively favored states are constrained. Genetic constraints occur when additive genetic variance in selectively favored directions is absent (absolute constraints) or present but small (quantitative constraints). Quantitative—unlike absolute—constraints are presumed surmountable given time. This ignores that a population might become extinct before reaching the favored state, in which case demography effectively converts a quantitative into an absolute constraint. Here, we derive criteria for predicting when such conversions occur. We model the demography and evolution of populations subject to optimizing selection that experience either a single shift or a constant change in the optimum. In the single-shift case, we consider whether a population can evolve significantly without declining or else declines temporarily while avoiding low sizes consistent with high extinction risk. We analyze when populations in constantly changing environments evolve sufficiently to ensure long-term growth. From these, we derive formulas for critical levels of genetic variability that define demography-caused absolute constraints. The formulas depend on estimable properties of fitness, population size, or environmental change rates. Each extends to selection on multivariate traits. Our criteria define the nearly null space of a population's \mathbf{G} matrix, the set of multivariate directions effectively inaccessible to it via adaptive evolution.

Keywords: quantitative genetics, optimizing selection, extinction, multivariate traits, nearly null space.

Introduction

Evolutionary constraints are factors that prevent a population from obtaining a target phenotype, such as one that maximizes fitness. The empirical study of constraints is often approached from a quantitative genetic perspective. As a result, several recent studies have explored standing patterns of heritable variation and covariation with the least amount of genetic variation and, hence, relatively little evolutionary potential (Kirkpatrick and Lofsvold 1992; Blows et al. 2004; Mezey and Houle 2005). These patterns are the opposite of evolutionary lines of least resistance (Schluter 1996); they are the directions in which

evolution would be expected to proceed the slowest in the short term. In the long term on a curved adaptive landscape, these are the directions along which the population will spend the most time evolving (e.g., Via and Lande 1985).

We have previously drawn a distinction between absolute and quantitative constraints (Houle 2001; Mezey and Houle 2005). A population's evolutionary potential is absolutely constrained if it completely lacks additive genetic variation in some direction in phenotype space. Such a constraint might consist of an absence of variation in a single trait or set of traits, although relatively few large quantitative genetic studies have failed to detect genetic variation in individual traits (Lewontin 1974). A more likely source of absolute constraint is an absence of variation in particular combinations of traits, for example, variation that allows a simultaneous increase in fecundity and viability. These combinations of traits, which are inaccessible to evolution, constitute a null space. Whatever the precise nature of an absolute constraint, it will result in a \mathbf{G} matrix of additive-genetic variances and covariances that is singular.

A quantitative constraint exists when the ability to respond to selection is present but limited. When genetic variation does exist in the direction of the selection gradient, it is often a matter of interpretation whether it is useful to regard evolution as constrained. On the one hand, virtually any pattern of genetic variation and covariation will quantitatively constrain evolution in the sense that the ability to respond to selection will be less than maximal (Clark 1987; Arnold 1992) or slower than some standard (Agrawal and Stinchcombe 2009). On the other hand, if the pattern of selection stays constant, "small" amounts of heritable variation may represent no constraint at all if selection is applied for a long enough period of time (Zeng 1988). A number of situations where such quantitative constraints are nevertheless biologically important have been suggested, such as the deflection of the course of evolution from one optimum to another (Steppan et al. 2002; Blows and Hoffman 2005).

We argue here that demographic limitations on a population can convert quantitative evolutionary constraints

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into insuperable barriers to adaptation. This can occur either because a population can fail to adapt sufficiently fast to avoid extinction or because selection cannot be arbitrarily strong without undermining the persistence of the population to which it is applied. Our main idea is that demographic consequences of adaptive change themselves impose evolutionary constraints, which we will call demographic evolutionary constraints. The novel aspect of our approach is that it explicitly considers the joint dynamics of evolution and population size, revealing the direct demographic consequences of slow adaptive change or strong selection.

The primary objective of this article, then, is to develop definitions of demographic constraints that can be applied to standing patterns of heritable variation in single and multivariate quantitative traits. We introduce the underlying concepts in the relatively simple case where fitness depends on a single quantitative trait and extend these to cases in which fitness depends on multiple traits, thereby defining a nearly null space for evolution. We consider three demographic criteria. The most stringent requires that a population not decline. The other two allow transient declines but require long-term growth or that population size remains above dangerously small levels.

Constraints for Single Traits

We begin developing our demographically based concepts of evolutionary constraints for a population in which fitness depends on a single phenotypic trait. Specifically, assume the population has discrete, nonoverlapping generations and that individual absolute fitness depends on a quantitative trait z subject to Gaussian optimizing selection: $W(z) = F \exp[-(1/2)(z - \theta)^2/\omega^2]$. Here, θ is the optimum phenotype and $1/\omega^2$ quantifies the strength of stabilizing selection. The parameter F is the maximum possible absolute fitness, that is, the number of descendants produced by an individual with the optimal phenotype. We assume fitnesses are density independent or nearly so, as might occur in a population well below carrying capacity.

If z has a normal distribution with mean \bar{z} and phenotypic variance σ_p^2 , then the mean fitness $\bar{W}(\bar{z})$ is

$$\bar{W}(\bar{z}) = \hat{F} \exp\left[-\frac{(\bar{z} - \theta)^2}{2\nu^2}\right], \quad (1)$$

where $\nu^2 = \omega^2 + \sigma_p^2$ and $\hat{F} = F(\omega^2/\nu^2)^{1/2} = F[\omega^2/(\omega^2 + \sigma_p^2)]^{1/2}$ (e.g., Gomulkiewicz and Holt 1995). We assume hard selection (see Wallace 1970) such that (density-independent) absolute mean fitness $\bar{W}(\bar{z})$ is also the population's finite per capita growth rate; growth is assured

so long as $\bar{W}(\bar{z}) \geq 1$. The quantity \hat{F} is the maximum possible rate of population growth when the mean phenotype is at the optimum; $\hat{F} < F$ because the existence of phenotypic variance ensures that individuals cannot all have the optimum phenotype θ .

We first consider evolutionary scenarios where a population starts evolving at a phenotype displaced from the optimum state θ , which remains fixed while the population either adapts or becomes extinct. We refer to this as the single-shift scenario, since we imagine that the displacement might arise from a single discrete change in the environment. This might occur, for example, as a result of the introduction or extinction of species with which the target species interacts. The single-shift scenario has been shown to yield the best fit among a collection of simple evolutionary models to an extensive database on phenotypic divergence (Estes and Arnold 2007).

Once the optimum shift occurs, adaptive evolution will move the population closer to its optimum phenotype and maximal mean fitness as long as there is additive genetic variance in the selected trait. To see this, consider the one-generation evolutionary response of the mean phenotype to Gaussian stabilizing selection $\Delta\bar{z} = \bar{z}_{t+1} - \bar{z}_t = \sigma_A^2(\theta - \bar{z}_t)/\nu^2$, where σ_A^2 is the additive-genetic variance for the trait (Lande 1976). From this and the identity $\sigma_p^2 = \sigma_A^2 + \sigma_E^2$, it follows that the distance from the optimum shrinks by a factor $1 - \sigma_A^2/\nu^2$ each generation and, indeed, that

$$d_t = \left(1 - \frac{\sigma_A^2}{\nu^2}\right)^t d_0, \quad (2)$$

where $d_t = |\bar{z}_t - \theta|$ is the distance from the optimum after t generations of selection. As a consequence, the population growth rate (eq. [1]) will increase monotonically to its maximum value \hat{F} provided that additive-genetic variance is not 0.

Under these idealized circumstances, evolution is unconstrained except in the complete absence of additive-genetic variation. Indeed, let $R_t = |\bar{z}_t - \bar{z}_0|$ be the magnitude of evolutionary divergence after t generations of adaptation. From equation (2),

$$R_t = d_0 - d_t = \left[1 - \left(1 - \frac{\sigma_A^2}{\nu^2}\right)^t\right] d_0. \quad (3)$$

Thus, any amount of adaptive divergence is theoretically possible, provided only that $\sigma_A^2 > 0$. However, evolution of the mean phenotype toward the new optimum matters only if the population does not become extinct before reaching that optimum.

*Constraints Imposed by Consistent Growth
under a Single Optimum Shift*

A population that never declines in size certainly avoids risking extinction. This sufficient requirement for persistence, in turn, imposes strict limitations on the size of the shift in the optimum after which a population can still grow. From equation (1), the boundary between population growth and decline is defined by $\overline{W} = \hat{F} \exp[-(1/2)d^2/\nu^2] = 1$, where $d = |\bar{z} - \theta|$. Rearranging this equation shows that a static population (i.e., one that is neither growing nor declining) must differ from the phenotypic optimum by amount

$$d_{\text{stat}} = \sqrt{\nu^2 \ln \hat{F}^2}. \quad (4)$$

Population size will fall whenever its mean phenotype is further than d_{stat} from the optimum and increase when it is closer.

The requirement that a population never declines means that $d_t \leq d_{\text{stat}}$ for all t . In the case of a single unchanging optimum, this requirement will be satisfied whenever the initial distance $d_0 \leq d_{\text{stat}}$. Incorporating this limit into equation (3) and using equation (4) shows that

$$R_t \leq \left[1 - \left(1 - \frac{\sigma_A^2}{\nu^2} \right)^t \right] \sqrt{\nu^2 \ln \hat{F}^2}. \quad (5)$$

The requirement that a population not decline thus limits its evolutionary divergence, even when $\sigma_A^2 > 0$. Indeed, the possible divergence is bounded above by $R_\infty = (\nu^2 \ln \hat{F}^2)^{1/2}$.

Inequality (5) can be used to formulate a definition of evolutionary constraint in terms of heritable genetic variation. Suppose there is a minimum amount of divergence, R_{min} , regarded as biologically relevant. For example, R_{min} might be the smallest statistically detectable change for a given feasible sample size or the smallest morphological difference needed to assign subspecific status. According to inequality (5), $R_t < R_{\text{min}}$ if the right-hand side of inequality (5) is less than R_{min} . Rearranging the latter inequality shows that the population will be constrained ($R_t < R_{\text{min}}$) whenever $\sigma_A^2 < \sigma_{A,\text{crit}}^2$, where

$$\sigma_{A,\text{crit}}^2 = \nu^2 (1 - \rho^{1/t}) \quad (6)$$

and $\rho = (R_\infty - R_{\text{min}})/R_\infty$. That is, a population's effective capacity to evolve in response to a single optimum shift is constrained by the requirement of consistent growth if σ_A^2 is smaller than $\sigma_{A,\text{crit}}^2$. The dimensionless parameter ρ ranges between 0 and 1 and indicates the ecological opportunity for evolving beyond the minimum divergence without declining in size.

The presence of time parameter t in constraint condition (6) limits its usefulness for assessing constraints to non-equilibrium populations. Still, there are a number of situations in which evolutionary biologists have an interest in the role of time-dependent constraints for ongoing evolution. These include mechanistic studies of rates of phenotypic divergence over geological time (e.g., Estes and Arnold 2007) and, in conservation biology, projecting capacities for rapid adaptive evolution in response to habitat destruction, invasion, or climate change (Bradshaw and Holzapfel 2006). Time-dependent constraints are of paramount importance to plant and animal breeders who seek to achieve breeding objectives in the shortest time.

Constraint (6) depends on three parameters that together define the Gaussian absolute fitness surface for a population: the "width" of the surface, $\nu^2 = \omega^2 + \sigma_p^2$; the distance to the optimum phenotype, $d = |\bar{z} - \theta|$; and the corresponding population growth rate, \overline{W} . Note that R_∞ can be estimated from these parameters since, from equation (1),

$$\nu^2 \ln \hat{F}^2 = \nu^2 \ln \overline{W}^2 + (\bar{z} - \theta)^2 = \nu^2 \ln \overline{W}^2 + d^2.$$

Many empirical studies report values of these parameters standardized by the phenotypic variance σ_p^2 (Kingsolver et al. 2001), so it is useful to recast constraint (6) in terms of heritability, $h_{\text{crit}}^2 = \sigma_A^2/\sigma_p^2$:

$$h_{\text{crit}}^2 = \tilde{\nu}^2 (1 - \rho^{1/t}) = \tilde{\nu}^2 \left[1 - \left(1 - \frac{\tilde{R}_{\text{min}}}{\sqrt{\tilde{\nu}^2 \ln \overline{W}^2 + \tilde{d}^2}} \right)^{1/t} \right], \quad (7a)$$

where $\tilde{\nu}^2 = \nu^2/\sigma_p^2$, $\tilde{d} = |\bar{z} - \theta|/\sigma_p$, and $\tilde{R}_{\text{min}} = R_{\text{min}}/\sigma_p$ are the variance-standardized, nondimensional values. Alternatively, the mean-standardized version of the constraint—the critical "evolvability" (Houle 1992)—is

$$I_{A,\text{crit}} = \check{\nu}^2 \left[1 - \left(1 - \frac{\check{R}_{\text{min}}}{\sqrt{\check{\nu}^2 \ln \overline{W}^2 + \check{d}^2}} \right)^{1/t} \right], \quad (7b)$$

where $\check{\nu}^2 = \nu^2/\bar{z}^2$, $\check{d} = |\bar{z} - \theta|/\bar{z}$, and $\check{R}_{\text{min}} = R_{\text{min}}/\bar{z}$. Both standardizations make assumptions about the scaling of variances to the population mean (for further information about this issue, see Hansen and Houle 2008).

As a practical point, parameters estimated from an experimental population can be used in constraint formula (6) to assess constraints for a wild population with a different mean phenotype, assuming that both share the same Gaussian absolute fitness surface. Experimental studies that have jointly estimated variance-standardized $\tilde{\nu}^2$ and

\tilde{d} suggest that the median values are, very roughly, $\tilde{v}^2 = 6.5$ and $\tilde{d} = 0.8$ (app. A). These same studies do not report corresponding finite growth rates, but it seems reasonable that the surveyed populations were not in decline, which implies $\bar{W} \geq 1$. We consider only such growth rates in our figures.

Figure 1 shows critical heritability (eq. [7a]) plotted versus divergence time t for $\tilde{R}_{\min} = 0.5$ phenotypic standard deviations. This value of \tilde{R}_{\min} corresponds to a between-population difference that would be detected with <80% power using a two-sample t -test, given a sample size of 50 and 5% significance level. The results indicate that few populations would diverge too little for statistical detection after 1,000 generations of evolution, but those with heritabilities <0.1 would fail to evolve detectable differences within 100 generations and, in that sense, are constrained.

Mayr (1969) proposed that subspecific rank be defined by a morphological difference of at least $\tilde{R}_{\min} = 2.6$ phenotypic standard deviations. According to inequality (5), the maximal possible variance-standardized response to selection is $\tilde{R}_{\infty} = (\tilde{v}^2 \ln \hat{F}^2)^{1/2} = (\tilde{v}^2 \ln \bar{W}^2 + \tilde{d}^2)^{1/2}$. Thus, if a population's absolute fitness surface were parameterized by ballpark values $\tilde{v}^2 = 6.5$, $\tilde{d} = 0.8$, and $\bar{W} < 1.6$, it could not attain subspecific rank under the single-shift scenario without experiencing a period of decline.

Constraints from Avoiding Low Population Size under an Optimum Shift

A population that falls in size is not necessarily doomed to extinction as long as the decline is temporary. However,

even a population capable of growth may readily become extinct if its numbers ever become small. This is because small population size is associated with extinction risks such as demographic stochasticity, Allee effects, and inbreeding. To avoid these risks, a population must, in addition to being capable of long-term growth, avoid dangerously low population sizes. We show how the demographic requirement of remaining above critically low population sizes imposes its own evolutionary constraint.

We develop this concept of constraint by adopting the same assumptions for population and evolutionary dynamics as in “Constraints Imposed by Consistent Growth under a Single Optimum Shift” but now assume that the population declines deterministically in size initially, so $\bar{W}(\tilde{z}_0) < 1$. Since mean fitness increases monotonically when $\sigma_A^2 > 0$, the decline should be only temporary. However, if the population reaches very low numbers in the course of adaptation, it may become extinct before mean fitness can recover to a level consistent with growth.

Gomulkiewicz and Holt (1995) analyzed this scenario. In their joint evolutionary-demographic model, N_t is population size at time t . Then $N_{t+1} = \bar{W}(\tilde{z}_t)N_t$, where $\bar{W}(\tilde{z}_t)$ is the mean fitness in generation t (eq. [1]). Rather than model extinction directly, they used an artifice, assuming the existence of a quasi extinction threshold size, N_q , below which the population would face a dramatically increased risk of immediate extinction. Quasi extinction thresholds are sometimes used in population viability analyses to represent the smallest population size above which Allee effects, demographic stochasticity, and inbreeding depression can be ignored (Lande et al. 2003).

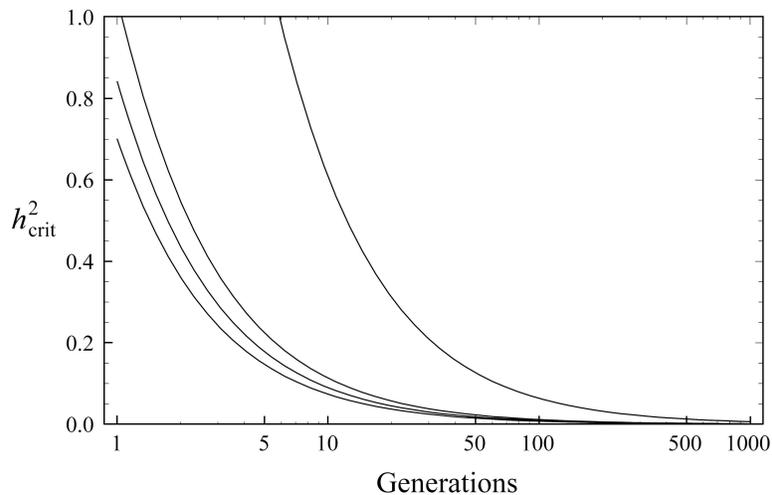


Figure 1: Log-linear plot of minimum heritabilities needed to evolve at least $\tilde{R}_{\min} = 0.5$ phenotypic standard deviations without population decline versus evolutionary time (eq. [7a]) for various assumptions regarding the growth rate of study populations. From right to left, curves correspond to $\bar{W} = 1, 2, 3$, and 5 , respectively. Other parameter values: $\tilde{v}^2 = 6.5$, $\tilde{d} = 0.8$.

Gomulkiewicz and Holt’s analyses showed that a population’s prospects of extinction depend on three factors: the initial rate of population decline, the ratio of initial to quasi extinction size, and the additive-genetic variance of the trait governing fitness. In the single-shift scenario, the initial rate of decline (or maladaptation) is positively related to the distance from the phenotypic optimum $\tilde{d}_0 = |\tilde{z}_0 - \theta|$ (see eq. [1]). Using equations (7) and (8) from Gomulkiewicz and Holt (1995) and variance-scaled parameter values, it can be shown that critical levels of each of these factors are determined implicitly by the untidy but useful equation

$$t_R \left(\ln \bar{W}^2 + \frac{\tilde{d}^2}{\tilde{v}^2} \right) - \frac{\tilde{d}_0^2}{\tilde{v}^2} \times \frac{1 - (1 - h_{crit}^2/\tilde{v}^2)^{2t_R}}{1 - (1 - h_{crit}^2/\tilde{v}^2)} = \ln \left(\frac{N_q}{N_0} \right)^2, \tag{8a}$$

where t_R is the time required for a population to evolve a growth rate that exceeds 1 and recover from its initial decline:

$$t_R = \frac{\ln(\tilde{v}^2 \ln \bar{W}^2 + \tilde{d}^2) - \ln \tilde{d}_0^2}{\ln [1 - (1 - h_{crit}^2/\tilde{v}^2)]}. \tag{8b}$$

The unscaled version of equations (8) has the same form but with the nondimensional parameters replaced by their untransformed values and with h_{crit}^2 replaced by $\sigma_{A,crit}^2$. The mean-standardized constraint takes the same form as well but with \tilde{v}^2 , \tilde{d} , and $\tilde{d}_0 = d_0/\bar{z}$ in place of \tilde{v}^2 , \tilde{d} , and \tilde{d}_0 , respectively, and with $I_{A,crit}$ taking the place of h_{crit}^2 .

Equations (8) can be used to solve for the minimum heritability h_{crit}^2 , consistent with remaining above dangerously low population sizes in terms of the other parameters. Populations with heritabilities less than h_{crit}^2 will face high extinction risks when the optimum undergoes a single shift of the size assumed. Note that, in contrast to equations (6) and (7), this definition does not require explicit specification of a minimal evolutionary response since that is determined by the requirement to remain above low densities. However, equations (8) do require additional input regarding the focal population’s initial size relative to the quasi extinction threshold, N_q/N_0 , and its initial deviation from the optimum, \tilde{d}_0 . (Estimates of \tilde{v}^2 , \tilde{d} , and \bar{W} can come from another population with the same Gaussian fitness surface.) Figure 2 illustrates the functional relationships between h_{crit}^2 and these two new parameters using the same estimates for the other parameters as above. These functions illustrate that the requirement of maintaining sufficient population size can impose severe constraints on evolution for populations that are relatively

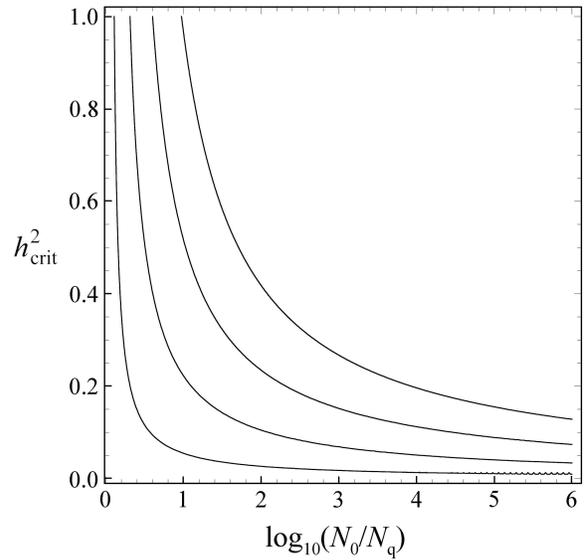


Figure 2: Minimum heritabilities consistent with avoiding low population size versus the order of magnitude of initial population size above the quasi extinction threshold (eqq. [8] with $\tilde{v}^2 = 6.5$, $\tilde{d} = 0.8$, $\bar{W} = 2$). From left to right, curves correspond to increasing initial distance from the optimum ($\tilde{d}_0 = 0.5, 1, 1.5,$ and 2 phenotypic standard deviations).

near quasi extinction or in steep decline (indicated by large \tilde{d}_0).

Constraints of Long-Term Persistence in a Changing Environment

Many populations face perpetually changing environments and will confront certain extinction unless they can continually adapt (e.g., Davis and Shaw 2001; Davis et al. 2005). The requirement of long-term persistence in a changing environment imposes its own form of evolutionary constraint. Consider the same model of optimizing selection as above but where the optimal phenotype θ changes through time. Bürger and Lynch (1995; see also Lynch and Lande 1993) showed among other things that if the optimum changes at rate k with time t , that is, $\theta_t = kt$, then long-term persistence is assured, provided that the asymptotic population growth rate, $\bar{W}_\infty = \hat{F} \exp[-(1/2)k^2 v^2/\sigma_A^4]$, exceeds 1. They used this expression to define a critical rate of environmental change beyond which a population would ultimately decline to extinction.

Bürger and Lynch’s expression can also be used to determine the minimum amount of additive variance needed to ensure long-term population growth in an environment changing at a given rate k . Setting \bar{W}_∞ equal to 1 and solving for σ_A^2 suggests a critical value of additive-genetic variance

below which a population will become asymptotically extinct:

$$\sigma_{A,\text{crit}}^2 = |k| \sqrt{\frac{\check{\nu}^2}{\ln \hat{F}^2}} \quad (9)$$

A phenotypic variance-scaled version of this equation is

$$h_{\text{crit}}^2 = |\check{k}| \sqrt{\frac{\check{\nu}^2}{\ln \hat{F}^2}} = |\check{k}| \frac{\check{\nu}^2}{\sqrt{\check{\nu}^2 \ln \bar{W}^2 + \check{d}^2}}, \quad (10a)$$

where $\check{k} = k/\sigma_p$ and the other parameters are as previously defined (fig. 3). The mean-standardized version of equation (9) is

$$I_{A,\text{crit}} = |\check{k}| \sqrt{\frac{\check{\nu}^2}{\ln \hat{F}^2}} = |\check{k}| \frac{\check{\nu}^2}{\sqrt{\check{\nu}^2 \ln \bar{W}^2 + \check{d}^2}}, \quad (10b)$$

where $\check{k} = k/\bar{z}$ and the other parameters are as defined above.

Equation (10a) shows that the critical heritability—and thus the degree of constraint—is directly proportional to the speed of environmental change. But since $h^2 \leq 1$, this obtains only until \check{k} reaches the value $\check{k}_{\text{max}} = (\check{\nu}^2 \ln \bar{W}^2 + \check{d}^2)^{1/2}/\check{\nu}^2$, above which it is impossible for any population, even one with perfect heritability, to evolve sufficiently fast to persist (fig. 3). This prohibitive rate may be quite low, as slow as 0.5 phenotypic standard deviations per generation for a population with Gaussian fitness surface parameters $\check{\nu}^2 = 6.5$, $\check{d} = 0.8$, and $\bar{W} = 2$.

Constraints on Multivariate Traits

The analyses above assume that selection is concentrated on a single trait, but individual fitness in real populations is generally determined by multiple correlated traits. We can show that the three basic formulations of effective evolutionary constraints derived above all apply to multivariate traits with the parameters reinterpreted in mathematically sensible ways. We illustrate these extensions by deriving expression (9) for constraints associated with asymptotic persistence in a changing environment. Derivations corresponding to consistent growth (eq. [6]) and avoiding low population size (the nonstandardized version of eqq. [8]) are provided in appendixes B and C, respectively.

We assume that individual absolute fitness now depends on a multivariate trait vector \mathbf{z} : $W(\mathbf{z}) = F \exp[-(1/2)(\mathbf{z} - \boldsymbol{\theta}_t)' \mathbf{W}^{-1}(\mathbf{z} - \boldsymbol{\theta}_t)]$, where the prime indicates transpose. The vector $\boldsymbol{\theta}_t$ is the multivariate optimum phenotype at time t , and the positive-definite matrix \mathbf{W} describes the pattern of

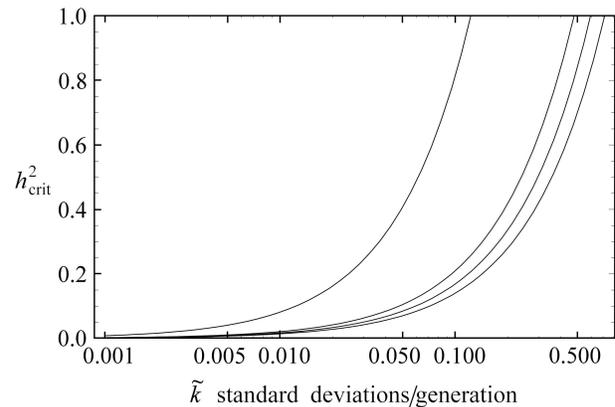


Figure 3: Log-linear plot of the minimum heritabilities needed to persist versus the rate of environment change \check{k} (eqq. [10]). From left to right, curves correspond to $\bar{W} = 1, 2, 3$, and 5 , respectively. Other parameters: $\check{\nu}^2 = 6.5$, $\check{d} = 0.8$.

multivariate selection, which we assume is constant. The parameter F is, as before, the fitness of an individual with the optimal phenotype. This Gaussian fitness function directly extends the one used above for a univariate trait.

If \mathbf{z} has a normal distribution at time t with mean $\bar{\mathbf{z}}_t$ and phenotypic covariance matrix \mathbf{P} , then the mean fitness/finite growth rate is

$$\bar{W}(\bar{\mathbf{z}}_t) = \hat{F} \exp\left[-\frac{1}{2}(\bar{\mathbf{z}}_t - \boldsymbol{\theta}_t)' \mathbf{V}^{-1}(\bar{\mathbf{z}}_t - \boldsymbol{\theta}_t)\right], \quad (11)$$

where $\mathbf{V} = \mathbf{W} + \mathbf{P}$ and $\hat{F} = F(|\mathbf{V}^{-1}\mathbf{W}|)^{1/2}$. ($|\mathbf{M}|$ denotes the determinant of a matrix \mathbf{M} .) The population grows whenever $\bar{W} > 1$.

Under the above assumptions, the one-generation multivariate evolutionary response to selection is $\Delta \bar{\mathbf{z}}_t = \bar{\mathbf{z}}_{t+1} - \bar{\mathbf{z}}_t = \mathbf{G}\boldsymbol{\beta}_t$, where \mathbf{G} is the additive-genetic covariance matrix underlying the distribution of \mathbf{z} and $\boldsymbol{\beta}_t = \mathbf{V}^{-1}(\boldsymbol{\theta}_t - \bar{\mathbf{z}}_t)$ is the selection gradient vector (Lande 1979). The principal components of \mathbf{G} are genetically uncorrelated directions in phenotype space (eigenvectors), and each direction is associated with an amount of additive-genetic variance (an eigenvalue). The component associated with the greatest amount of variation has been called the “evolutionary line of least resistance,” since selection of a given strength applied in that direction would produce the largest evolutionary response (Schluter 1996).

For evolutionary constraints, our interest is, rather, in the principal components of \mathbf{G} with the smallest amounts of genetic variation, since in these directions, selection could yield too little evolution. They are the evolutionary lines of highest resistance and, if directional selection is independent of variation, also represent a population’s

greatest vulnerability to extinction. Let the eigenvalues of \mathbf{G} arranged in decreasing order be $\sigma_{A1}^2 \geq \sigma_{A2}^2 \geq \dots \geq \sigma_{An}^2 \geq 0$, with associated unit eigenvectors (PC loadings) $\mathbf{g}_1, \mathbf{g}_2, \dots, \mathbf{g}_n$. Direction \mathbf{g}_1 is the evolutionary line of least resistance (i.e., Schluter's \mathbf{g}_{\max}), but a population's slowest adaptive responses will occur when selection of a given strength is applied in direction \mathbf{g}_n .

Now consider the demographic consequences of a population in a changing environment. To be concrete, let the optimal phenotype at time t be $\theta_t = t\mathbf{k}$, where the elements of \mathbf{k} are the rates of change for each component of the multivariate optimum.

From equation (11), the finite growth rate at time t is

$$\bar{W}(\bar{\mathbf{z}}_t) = \hat{F} \exp \left[-\frac{1}{2} (\bar{\mathbf{z}}_t - t\mathbf{k})' \mathbf{V}^{-1} (\bar{\mathbf{z}}_t - t\mathbf{k}) \right]. \quad (12)$$

Iterating $\Delta \bar{\mathbf{z}}_t = \mathbf{G}\beta_t = \mathbf{G}\mathbf{V}^{-1}(t\mathbf{k} - \bar{\mathbf{z}}_t)$ gives $\bar{\mathbf{z}}_t = (\mathbf{I} - \mathbf{G}\mathbf{V}^{-1})^t \bar{\mathbf{z}}_0 + t\mathbf{k} - [\mathbf{I} - (\mathbf{I} - \mathbf{G}\mathbf{V}^{-1})^t] \mathbf{V}\mathbf{G}^{-1}\mathbf{k}$, where \mathbf{I} is the identity matrix. We have

$$\bar{\mathbf{z}}_t \rightarrow t\mathbf{k} - \mathbf{V}\mathbf{G}^{-1}\mathbf{k} \quad (13)$$

as $t \rightarrow \infty$, so asymptotically, the growth rate (eq. [12]) is constant, $\bar{W}_\infty = \hat{F} \exp[-(1/2)\mathbf{k}'\mathbf{G}^{-1}\mathbf{V}\mathbf{G}^{-1}\mathbf{k}]$.

Long-term persistence is assured, provided $\bar{W}_\infty \geq 1$. This is equivalent to requiring

$$\mathbf{k}'\mathbf{G}^{-1}\mathbf{V}\mathbf{G}^{-1}\mathbf{k} \leq \ln \hat{F}^2. \quad (14)$$

The (scalar) quantity $\mathbf{k}'\mathbf{G}^{-1}\mathbf{V}\mathbf{G}^{-1}\mathbf{k}$ is bounded above by $k^2\nu^2/\sigma_{An}^4$, where ν^2 is the largest eigenvalue of \mathbf{V} , σ_{An}^2 is the smallest eigenvalue of \mathbf{G} , and $|k| = (\mathbf{k}'\mathbf{k})^{1/2} = \|\mathbf{k}\|$ is the length of the vector \mathbf{k} . Substituting this upper bound into the left-hand side of equation (14) shows that $\sigma_{An}^2 \geq |k|(\nu^2/\ln \hat{F}^2)^{1/2}$ is a sufficient condition for asymptotic persistence in a linearly changing environment.

This demonstrates that, with $|k|$ and ν^2 defined appropriately, the threshold (eq. [9]) can be used to characterize demographic constraints in a changing environment when fitness and population growth are governed by multivariate traits. That is, if any principal component of \mathbf{G} has variance (eigenvalue) less than $\sigma_{A,\text{crit}}^2 = |k|(\nu^2/\ln \hat{F}^2)^{1/2}$, the population lacks the capacity to respond to some patterns of selection induced by environmental change without becoming extinct. Interpretation of $|k|$ is straightforward when components of phenotype \mathbf{z} are measured using the same units, in which case $|k|$ is the overall speed of movement of the optimum in multivariate space. This simplicity breaks down, however, if components have different units (e.g., mm and g). In that case, phenotypes should be mean or variance standardized first, as we now discuss.

Normalized versions of the constraint criteria can be

obtained by introducing a standardization matrix. For example, the diagonal matrix \mathbf{N} with entries equal to the square roots of the diagonal entries of \mathbf{P} can be used to standardize values relative to phenotypic variances: $\Delta \tilde{\mathbf{z}} = \mathbf{N}^{-1}\Delta \mathbf{z}$, $\tilde{\theta} = \mathbf{N}^{-1}\theta$, $\tilde{\mathbf{V}} = \mathbf{N}^{-1}\mathbf{V}\mathbf{N}^{-1}$, and $\tilde{\mathbf{H}} = \mathbf{N}^{-1}\mathbf{G}\mathbf{N}^{-1}$. These standardizations are equivalent to those discussed by Hansen and Houle (2008), who used element-wise operations instead of standard matrix and vector multiplication.

The matrix $\tilde{\mathbf{H}}$ is a sort of heritability matrix, with heritabilities of individual traits along the diagonal. Constraints (10) would then apply, with h_{crit}^2 referring to the smallest eigenvalue of $\tilde{\mathbf{H}}$, $\tilde{\nu}^2$ referring to the largest eigenvalue of $\tilde{\mathbf{V}}$, $\tilde{d} = \|\mathbf{N}^{-1}\mathbf{d}\|$, and $|\tilde{k}| = \|\mathbf{N}^{-1}\mathbf{k}\mathbf{c}\| = |k|\|\mathbf{N}^{-1}\mathbf{c}\|$, where $\mathbf{c} = \mathbf{k}/|k|$.

Parallel results and interpretations apply, given other standardization schemes. For example, in defining the effective dimensionality of multivariate evolution, Kirkpatrick (2008) considers traits standardized by their means, in which case \mathbf{N} is a diagonal matrix with the mean values along the diagonal. He observes that the matrix $\tilde{\mathbf{H}}$ can be factored into the product \mathbf{ERE} of nondimensional matrices, where \mathbf{E} is a diagonal matrix containing the evolvability of each trait (Houle 1992) and \mathbf{R} is the matrix of additive-genetic correlations. Constraints are present if any eigenvalue of this matrix product is less than $I_{A,\text{crit}}$, computed using equation (10b) with mean-standardized values.

Another way to connect multivariate constraints to the univariate formula (9) is to note from equation (13) that for large enough t , $\mathbf{z}_t \approx t\mathbf{k}$. That is, a population adapting to an optimum changing in a fixed direction \mathbf{k} will ultimately evolve only in that direction. Thus, the response to selection is asymptotically one-dimensional, and the additive-genetic variance relevant for adaptation along this line is the conditional genetic variance along \mathbf{k} (Hansen et al. 2003; Hansen and Houle 2008), $(\mathbf{c}'\mathbf{G}^{-1}\mathbf{c})^{-1}$, where $\mathbf{c} = \mathbf{k}/|k|$ is a unit vector pointing in the direction the optimum moves. By equation (9), persistence is assured if this conditional genetic variance exceeds the critical value $|k|(\nu^2/\ln \hat{F}^2)^{1/2}$, where now $1/\nu^2 = \mathbf{c}'\mathbf{V}^{-1}\mathbf{c}$ quantifies the strength of stabilizing selection applied along the asymptotic direction of evolution.

Discussion

To evolve, a population obviously must persist, and this fact can restrict capacity for adaptive evolution. We have developed formulas to quantify how the potential for evolution is constrained by the need to avoid extinction. These demographic constraints are expressed as threshold amounts of additive genetic variance below which populations are in effect constrained. The thresholds depend

on features of the adaptive landscape that can be estimated without genetic analysis, and thus they provide a priori standards against which measured additive genetic variation can be compared.

Our demographic constraints have somewhat different interpretations than absolute constraints (Houle 2001; Mezey and Houle 2005), which are caused by an absence of genetic variation. Any extant population may be subject to an absolute constraint that holds its mean fitness below what it hypothetically would be were the constraint absent. In contrast, the demographic constraints derived above describe patterns of selection that could not have been experienced by the population in the past and predict patterns of selection the population could not survive in the near future, given our working assumptions.

It is easier to interpret and generalize amounts of variation on a standardized scale. Both variance and mean standardizations are informative; however, we have restricted our interpretations of existing data to a variance-standardized scale and therefore to critical heritabilities because previous estimates of the width of stabilizing selection functions have been reported on a variance-standardized scale.

Studies of wild and laboratory populations have found that heritabilities for fitness-related traits vary widely, with an average value of about 0.2–0.3 (Mousseau and Roff 1987; Houle 1992). This average is comfortably above the ballpark threshold values computed for our three main scenarios under many—but not all—conditions (figs. 1–3). However, almost 20% of fitness-related heritability estimates are <0.1 (fig. 5 of Mousseau and Roff 1987). This means that adaptive evolution in a substantial fraction of populations might be restricted by demographic requirements. Indeed, Janzen (1994) estimated $h^2 = 0.1$ for the threshold temperature of sex determination and predicted that it will prove inadequate for maintaining viable sex ratios in a population of painted turtles (*Chrysemys picta*), given projected increases in climatic temperatures. Similarly, Willi and Hoffman (2008) used stochastic simulations based on the study by Bürger and Lynch (1995) and parameter estimates derived from lab-reared populations of *Drosophila burchii* to predict that a heritability <0.1 in heat-knockdown resistance would not be enough to prevent extinction in populations of size 20 in a warming environment.

It has long been recognized that the potential for adaptive evolution suggested by heritabilities of isolated traits may be severely overstated as a result of genetic correlations among fitness-related traits (Dickerson 1955; Crow 1970). Empirical studies have found that natural selection often targets less variable combinations of traits (Etterson and Shaw 2001; Blows et al. 2004). When fitness depends on multiple correlated traits, the genetic capacity to re-

spond to selection is best described by the eigenvalues of the **G** matrix (or a dimensionless version of it). Absolute evolutionary constraints are present in a population if its **G** matrix has a zero eigenvalue since the population can fail completely to respond to directional selection (Kirkpatrick and Lofsvold 1992). That is, there are multivariate directions in which the population cannot evolve.

Unfortunately, estimation and statistical testing can never establish the absence of variation, including zero eigenvalues. The best that can be done is to demonstrate that an eigenvalue is likely to be smaller than some positive value. Even doing this has proven highly problematic in practice as a result of poor precision, downward bias, and dubious assumptions of procedures used to estimate the smallest eigenvalues (Houle 2001; Mezey and Houle 2005; Hine and Blows 2006; Kirkpatrick 2008; Meyer and Kirkpatrick 2008). The demography-based constraint criteria developed here may alleviate some of those practical issues by providing critical genetic variances >0 that can be rejected by statistical tests. When estimates of small eigenvalues are downward biased, then if all eigenvalues exceed a given threshold, one can be confident that the population is not constrained by that aspect of demography.

Estimates show, and neutral evolution models predict, that **G** matrices often have at least some very small eigenvalues (Kirkpatrick et al. 1990; Mezey and Houle 2005; Griswold et al. 2007), which implies that it may be common for evolution of multivariate traits to be channeled primarily along just a few dimensions (Schluter 1996; McGuigan et al. 2005). Likewise, some studies that estimate dimensionality (matrix rank) directly have been unable to reject the hypothesis of reduced rank (Kirkpatrick and Meyer 2004; Hine and Blows 2006). In a survey of several data sets, Kirkpatrick (2008) noted that the effective number of dimensions of multivariate genetic variation (defined by him as the sum of the eigenvalues of **G** divided by the largest eigenvalue) consistently lies between 1 and 2.

In theory, a reduced-rank matrix must have zero eigenvalues, so a **G** matrix of low dimension should indicate absolute genetic constraints. However, statistical approaches that utilize reduced-rank estimates of **G** are not well suited for revealing the nature of absolute constraints because they aim to account maximally for patterns of variation and covariation using as few dimensions as possible. By design, they “often discard information about phenotypic dimensions for which there is a small but non-zero amount of genetic variation” (Kirkpatrick and Meyer 2004, p. 2305). Thus, an estimate of low dimensionality need not imply a long-term adaptive constraint if the true absolute size of any statistically undetected eigenvalue of **G** is sufficiently large to forestall extinction. In that case, virtually any amount of evolutionary change would be

possible, given selection and enough time. Our consideration of the demographic consequences of adaptation shows that even a \mathbf{G} matrix of full rank does not guarantee the absence of evolutionary constraints.

The ability to estimate small eigenvalues of \mathbf{G} with statistical confidence is limited by the number of families one can accommodate in an empirical study (Mezey and Houle 2005). A partial way to overcome this obstacle is to use the fact that the eigenvalues of the phenotypic covariance matrix \mathbf{P} dominate the eigenvalues of \mathbf{G} (app. D; for an empirical demonstration, see McGuigan and Blows 2007). Thus, if \mathbf{P} has an eigenvalue smaller than a given critical value, then so must \mathbf{G} . Because sample size rather than family number limits statistical precision of estimates of \mathbf{P} , it may be possible to infer, on the basis of the eigenvalues of \mathbf{P} , that \mathbf{G} has an eigenvalue that is truly smaller than a given threshold rather than just statistically undetectable. This approach will, however, be inconclusive about constraints if all eigenvalues of \mathbf{P} are above the threshold.

The eigenvectors associated with zero eigenvalues form a basis for the null space of a matrix (Strang 1988). Applied to \mathbf{G} , the null space delimits directions that are inaccessible to evolution (Kirkpatrick and Lofsvold 1992). By extension, we define the nearly null space of \mathbf{G} as the multivariate space spanned by eigenvectors associated with eigenvalues that are consistent with demographic constraints. While these directions may allow some evolution, there is substantial risk that the evolution may be undone by extinction, the ultimate limitation.

Our models of population dynamics assume density-independent growth. Thus, our formulas are most relevant when applied to populations well below carrying capacity, as for many of those facing the prospect of extinction through environmental change or when colonizing a new habitat. In that case, our formulas will describe constraints most accurately for populations with density-independent growth up to a ceiling (e.g., Lande 1993) but should also provide excellent approximations for populations subject to negative density dependence at all sizes. For populations that experience strong density dependence at low numbers (such as Allee effects), the expressions represent lower bounds for constraints.

Our formulas are probably not applicable to strongly regulated populations that are near carrying capacity. Evolutionary constraints in such populations are determined chiefly by consequences of the abundances at which they are regulated (for mutational input, random genetic drift, and structuring of selection) rather than by extinction. The effects of population size on adaptation are often analyzed assuming soft selection (see Wallace 1970) such that the nature of density regulation is unaffected by evolution. By comparison, our focus on populations well below carrying capacity and in which adaptive evolution directly determines

population dynamics (i.e., hard selection) highlights how extinction can factor into genetic constraints.

The constraint formulas we derived rely on many other genetic and demographic simplifications. These include assuming that individual fitness is a Gaussian function of phenotype and that populations are normally distributed. Our models also ignore the effects of drift, selection, mutation, and linkage on the evolutionary dynamics of additive-genetic variation and covariation. They assume the absence of demographic and environmental stochasticity. Some of these assumptions might be valid, or approximately so, for some populations. For example, many real fitness functions can be locally approximated by Gaussian fitness functions. Other assumptions that are almost certainly not met we would expect to increase the severity of constraints above the levels implied by our formulas. For example, increases in the strength of selection and drift due to any reductions in population size should erode genetic variation available for evolution and thus slow the rate of adaptation, at least in the short run. Similarly, environmental and demographic stochasticity can undermine the persistence of populations that would otherwise be expected to persist. To the extent that these genetic and demographic features hinder adaptation and persistence relative to our biologically simplistic models, the criteria we have derived should understate the constraints imposed by population dynamics. However, further work is needed to clarify how violating these and other key assumptions, such as the multivariate normal distribution of breeding values, would affect our results.

This study explores a new direction within evolutionary demography, an emerging field that considers the feedback between evolutionary and population dynamics (reviewed in Day 2005). Previous work in “evo-demo” has considered the influence of evolution on population and community dynamics (e.g., Kinnison and Hairston 2007; Willi and Hoffman 2008) or how demographic context influences patterns of selection (e.g., Metcalf and Pavard 2006). Our study, by comparison, demonstrates how demography can limit the genetic potential of populations for adaptive evolution.

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APPENDIX A

Ballpark Gaussian Fitness Surface Parameter Estimates

Estimates of the Gaussian fitness surface (eq. [1]) can be obtained from phenotypic selection studies that jointly estimate the parameters ν^2 , d , and \bar{W} . To obtain rough empirical values, we used Estes and Arnold's (2007) joint estimates of variance-standardized $\tilde{\nu}^2$ and \tilde{d} that they extracted from the database on phenotypic selection studies compiled by Kingsolver et al. (2001). We further narrowed those to cases indicating stabilizing selection regardless of statistical significance. Stinchcombe et al. (2008) found that about 80% of the studies surveyed by Kingsolver et al. (2001) underestimate gamma, the stabilizing selection gradient, by a factor of 2, but they did not identify those studies. To compensate, we created a worksheet of the pared-down estimates and doubled each original gamma estimate with probability 0.8. Our ballpark values were obtained from recalculating the worksheet many times and noting median values based on the randomly corrected parameters. Changing the doubling probability had little effect on the results.

APPENDIX B

Multivariate Constraints Consistent with Growth

In this appendix, we show that equation (6) can be used to define evolutionary constraints consistent with population growth in a constant environment following a shift in the optimum when fitness is determined by a multivariate trait. We use the same model as that leading to equation (11) but assume that the phenotypic optimum is fixed, $\theta_t = \theta$. Let $\mathbf{d}_t = \bar{\mathbf{z}}_t - \theta$ denote the vector from the optimum to the population mean and $\|\mathbf{d}_t\|$ its length. Growth is assured, provided that $\bar{W}_t = \hat{F} \exp[-(1/2)\mathbf{d}_t^T \mathbf{V}^{-1} \mathbf{d}_t] \geq 1$ or, equivalently, $\mathbf{d}_t^T \mathbf{V}^{-1} \mathbf{d}_t \leq \ln \hat{F}^2$. The quadratic form on the left-hand side is bounded below by $\|\mathbf{d}_t\|^2/\nu^2$, where ν^2 is the largest eigenvalue of \mathbf{V} , so a necessary condition for growth is $\|\mathbf{d}_t\|^2 \leq \nu^2 \ln \hat{F}^2$ for all t . That is, to avoid declines, a population must never stray more than a distance $(\nu^2 \ln \hat{F}^2)^{1/2}$ from the optimum phenotype. It follows from the one-generation recursion $\Delta \bar{\mathbf{z}}_t = \mathbf{G}\beta_t = -\mathbf{G}\mathbf{V}^{-1}\mathbf{d}_t$ that $\|\mathbf{d}_{t+1}\| \leq \|\mathbf{d}_t\|$ so that the condition necessary for growth reduces to $\|\mathbf{d}_0\| \leq (\nu^2 \ln \hat{F}^2)^{1/2}$.

Consider next the response to selection. We measure the overall size of evolutionary change after t generations by $R_t = \|\bar{\mathbf{z}}_t - \bar{\mathbf{z}}_0\|$. The one-generation recursion for the

mean phenotype suggests that the smallest conceivable evolutionary response occurs when selection targets the direction of the smallest eigenvalue of \mathbf{G} , $\sigma_{\Lambda_n}^2$, governed at its weakest strength $1/\nu^2$, where ν^2 is the largest eigenvalue of \mathbf{V} . This will occur when \mathbf{d}_t is an eigenvector of \mathbf{G} corresponding to σ_n^2 and simultaneously an eigenvector of \mathbf{V} corresponding to ν^2 . Given this perfect storm of circumstances, $\Delta \bar{\mathbf{z}}_t = \Delta \mathbf{d}_t = -\sigma_{\Lambda_n}^2/\nu^2 \mathbf{d}_t$ and thus $\mathbf{d}_t = (1 - \sigma_{\Lambda_n}^2/\nu^2)^t \mathbf{d}_0$. Since $\bar{\mathbf{z}}_t - \bar{\mathbf{z}}_0 = \mathbf{d}_t - \mathbf{d}_0$, the magnitude of evolutionary response after t generations in this extreme case is $R_t = [1 - (1 - \sigma_n^2/\nu^2)^t] \|\mathbf{d}_0\|$. This shows that substantial evolution can occur even in this most prohibitive scenario if the initial distance from the optimum, $\|\mathbf{d}_0\|$, is large enough. However, the requirement of growth necessary constrains this distance to be less than $(\nu^2 \ln \hat{F}^2)^{1/2}$, and hence, the overall evolutionary response is bounded: $R_t \leq [1 - (1 - \sigma_n^2/\nu^2)^t] (\nu^2 \ln \hat{F}^2)^{1/2}$. If this upper bound is itself below the minimum amount of response recognized as biologically nontrivial, R_{\min} , then evolution can be constrained. It follows that constraints are present if any eigenvalue of \mathbf{G} is less than the critical value defined in equation (6), with ν^2 the largest eigenvalue of $\mathbf{V} = \mathbf{W} + \mathbf{P}$.

APPENDIX C

Multivariate Constraints Consistent with Avoiding Small Numbers

Here we show that the nonstandardized version of equations (8) applies to constraints for multivariate traits imposed by the requirement that a population avoid critically low sizes after a single shift in the optimum. If a population can manage this when selection is at its least effective and evolutionary responses are at their slowest, then there are, in essence, no evolutionary constraints. Otherwise, there are. Recalling the results of appendix B, we have

$$\begin{aligned} \bar{W}_t &= \hat{F} \exp \left[-\frac{1}{2} \left(1 - \frac{\sigma_{\Lambda_n}^2}{\nu^2} \right)^{2t} \mathbf{d}_0^T \mathbf{V}^{-1} \mathbf{d}_0 \right] \\ &= \hat{F} \exp \left[-\frac{\|\mathbf{d}_0\|^2}{2\nu^2} \left(1 - \frac{\sigma_{\Lambda_n}^2}{\nu^2} \right)^{2t} \right]. \end{aligned}$$

The second equality holds because the worst case scenario assumes that \mathbf{d}_0 is an eigenvector of \mathbf{V}^{-1} for its smallest eigenvalue $1/\nu^2$. This gives

$$\begin{aligned} N_t &= N_0 \prod_{i=0}^{t-1} \bar{W}_i = N_0 \hat{F}^t \exp \left[-\frac{\|\mathbf{d}_0\|^2}{2\nu^2} \sum_{i=0}^{t-1} \left(1 - \frac{\sigma_{\Lambda_n}^2}{\nu^2} \right)^{2i} \right] \\ &= N_0 \hat{F}^t \exp \left[-\frac{\|\mathbf{d}_0\|^2}{2\nu^2} \frac{1 - (1 - \sigma_{\Lambda_n}^2/\nu^2)^{2t}}{1 - (1 - \sigma_{\Lambda_n}^2/\nu^2)^2} \right]. \end{aligned}$$

Note too that the time t_R required to evolve growth assuming $\overline{W}_0 < 1$ satisfies $\overline{W}_R = 1$ (cf. eq. [8b]). From these considerations, it can be shown that the minimum amount of additive-genetic variance consistent with avoiding quasi extinction can be determined from equations (8) using nonstandardized versions of the parameters and substituting the smallest eigenvalue σ_{An}^2 of \mathbf{G} for h^2 with the understanding that ν^2 is the largest eigenvalue of $\mathbf{V} = \mathbf{W} + \mathbf{P}$ and $d_0 = \|\mathbf{d}_0\|$ is the initial distance from the population mean to the optimum. If any principal component of \mathbf{G} has additive-genetic variance (eigenvalue) smaller than this minimum, then a population's capacity to adapt is effectively constrained since there are situations in which it would reach population sizes so low as to face high risks of extinction.

APPENDIX D

Eigenvalues of \mathbf{P} versus Those of \mathbf{G}

We show here that the eigenvalues of \mathbf{P} dominate those of \mathbf{G} , generalizing Pease and Bull (1988), who proved that if \mathbf{P} has a zero eigenvalue, then so must \mathbf{G} . Let λ_p be an eigenvalue of \mathbf{P} with unit eigenvector \mathbf{v} . Recalling that $\mathbf{P} = \mathbf{G} + \mathbf{E}$, $\lambda_p = \mathbf{v}'\mathbf{P}\mathbf{v} = \mathbf{v}'\mathbf{G}\mathbf{v} + \mathbf{v}'\mathbf{E}\mathbf{v}$. Since \mathbf{E} is positive semidefinite, $\mathbf{v}'\mathbf{E}\mathbf{v} \geq 0$ (Strang 1988, p. 339), and so $\lambda_p \geq \mathbf{v}'\mathbf{G}\mathbf{v}$. But $\mathbf{v}'\mathbf{G}\mathbf{v} \geq \lambda_{An}$ where λ_{An} is the smallest eigenvalue of \mathbf{G} since \mathbf{v} is a vector of unit length (Strang 1988). Thus, $\lambda_p \geq \lambda_{An}$; that is, every eigenvalue of \mathbf{P} is bounded below by at least one eigenvalue of \mathbf{G} . A similar argument proves that no eigenvalue of \mathbf{G} can be greater than all eigenvalues of \mathbf{P} .

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Young elk at a Yellowstone hot spring (photograph by David Houle).