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A new way to integrate selection when both demography and selection gradients vary over time

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Abstract

When both selection and demography vary over time, how can the long-run expected strength of selection on quantitative traits be measured? There are two basic steps in the proposed new analysis: one relates trait values to fitness components and the other relates fitness components to total fitness. We used one population projection matrix for each state of the environment together with a model of environmental dynamics, defining total fitness as the stochastic growth rate. We multiplied environment-specific, stage-specific mean-standardized selection gradients by environment-specific, stage-specific elasticities of the stochastic growth rate, summing over all relevant life history and environmental paths. Our two example traits were floral tube length in a rainforest herb and the timing of birth in Red Deer. For each species, we constructed two models of environmental dynamics, including one based on historical climate records. We found that total integrated selection, as well as the relative contributions of life-history pathways and environments, varied with environmental dynamics. Temporal patterning in the environment has selective consequences. Linking models of environmental change to relevant short term data on demography and selection may permit estimation of the force of selection over the long-term in variable environments.

Keywords

variable selection gradients; environment-specific elasticity; structured populations; integrated elasticity; climate and demography

Introduction

This paper addresses the question: when both selection and demography vary over time in a structured population with overlapping generations, how can we measure the long-run expected strength of selection on quantitative traits? Included is the issue of how selection acting through different fitness components and in different states of the environment contributes to total selection. MacArthur (1968) may have been the first to consider selection for structured populations in variable environments for which population dynamics are modeled by projection matrices. He addressed selection on matrix elements themselves rather than on quantitative traits that influence matrix elements. Nevertheless, his paper, as well as later work by Caswell and Trevisan (1994), Horvitz et al. (2005), Caswell (2005), and Aberg et al. (2009) drew attention to the idea that, for a structured population in a variable environment, the effect on selection of perturbing a particular life history transition rate depends upon the current environmental state and the sequence of states in which it is embedded. Meanwhile, van Tienderen (2000), working with structured populations in constant environments, proposed the concept of *integrated elasticity* to integrate mean-standardized selection on a trait over the entire life cycle. He included, for example, selection acting through survival at different ages or selection acting through reproduction.

Here, we build in another layer of complexity experienced by many organisms: selection may also vary over time among environments in addition to over the life cycle (Siepielski et al. 2009). The issue we address in this paper focuses on the maps between phenotype, demography and fitness. We make a straightforward extension of van Tienderen's approach made possible by the development of new analytical tools in stochastic demography (Horvitz et al. 2005, Haridas and Tuljapurkar 2005). We apply our extended concept of *integrated selection* to quantitative traits measured in two well-studied systems, floral tube length in a neotropical rainforest herb (Horvitz and Schemske 1995, Schemske and Horvitz 1989) and the timing of birth in red deer (Coulson et al. 2003, Coulson and Tuljapurkar 2008). The present analysis differs from that in Coulson and Tuljapurkar (2008) in several important ways. First, their analysis applied methods for retrospective analysis, in which the trait distribution was observed each year and changes in trait distribution accumulated over the lifetime. The goal of their analysis was to determine explicit contributions during each year to the total changes over the life time. Here, in contrast, we address prospective questions about the long-term effects of all components of selection, by studying how an overall fitness measure varies with the underlying trait distribution. We consider the stochastic growth rate as a function of a quantitative trait, an approach that complements retrospective analysis.

Our results reveal that the strength of selection on a trait depends upon the environmental process that determines the sequence and frequency of environmental states. By environmental process we mean the type of underlying driver (e.g., climate cycles, successional processes, long-term constancy,...) that describes the environmental dynamics, determining the pattern of temporal variability in demography and selection pressures. Perhaps the most important implication is that an understanding of environmental variability and the process that generates it is necessary to be able to measure expected long-run

selection. A significant corollary is that any alteration of environmental drivers (climate, fires, floods, etc) will also impact the strength of selection on traits.

As in van Tienderen, there are two basic steps in the analysis: one relates trait values to fitness components and the other relates fitness components to total fitness. In a constant environment, the case considered by van Tienderen, fitness components are given by matrix elements (or lower level vital rates that are used to construct matrix elements) of a population projection matrix whose dominant eigenvalue ($\lambda = e^r$) measures average total fitness of a population. In a variable environment, the case studied here, we use one population projection matrix for each state of the environment together with a model of environmental dynamics that defines a stochastic sequence of environmental states (as in Horvitz et al. 2005) and use $\lambda_S = e^a$ as the measure of average total fitness for stochastic environments. Previous theory for structured populations established that, for density-independent population dynamics in deterministic environments, fitness is measured by the Lotka growth rate r (Charlesworth 1974, 1980, 1993, 1994 and Lande 1982) and that in stochastic environments it is measured by the stochastic growth rate a (Tuljapurkar 1982b, 1990). To relate trait values to demographic rates we use mean-standardized regression coefficients (analogous to selection gradients typically calculated for one episode of selection at a time in unstructured populations).

To estimate total integrated selection on the mean trait value over stages and environments, in this paper we employ a straightforward extension of van Tienderen's deterministic approach. We illustrate its implementation, but we do not present its proof in this paper. For each matrix element in each state of the environment we determine the regression relationship between the trait and the individual fitness component (Lande and Arnold 1983, Hereford et al. 2004). We multiply these environment-specific, stage-specific regression coefficients by environment-specific, stage-specific elasticities of the stochastic growth rate (Tuljapurkar et al. 2003, Horvitz et al. 2005, Haridas and Tuljapurkar 2005, Caswell 2005, Aberg et al. 2009) and sum over all relevant life history and environmental paths. Different subtotals address, for example, how selection differs among environmental states or among types of life history transitions.

This approach is timely and its implementation over more study systems may provide, new insights about patterns and strengths of selection in the wild. Sieplieski et al.(2009) recently provided the first review of temporal variability in selection, emphasizing the importance of the temporal perspective and concluding that, although selection is weak in most years and frequently changes sign, it is occasionally very strong. However, they did not propose a method to integrate such variability across time. The invaluable comprehensive review of selection in the wild by Kingsolver et al. (2001) summed up a decade and a half of studies that had been carried out since the mid 1980's, when seminal papers by Lande (1979), Lande and Arnold (1983) Arnold and Wade (1984a, b) made measuring selection in the wild accessible to field ecologists and evolutionary biologists. This extensive review did not contain many studies with temporal replication and it contained only a handful of studies that used total fitness rather than fitness components. Their conclusions are thus based overwhelmingly on selection evaluated in terms of single fitness components from single years, although there is extensive consideration of selection acting indirectly through

correlated quantitative traits. It remains to be seen whether the patterns they discerned will be altered by examining selection in a broader temporal, experiential and population context that includes changes over time at both the individual and population level due to environmental dynamics.

Methods

Methods: Demographic model

Consider a stage-structured population with S distinct life history stages censused at discrete times $t, t + 1$, and so on. At time t the number $N_i(t)$ of individuals in each stage i is given in the vector $\mathbf{N}(t)$. The population dynamics are given by $\mathbf{N}(t+1) = \mathbf{A}(t) \mathbf{N}(t)$, where $\mathbf{A}(t)$ is an $S \times S$ population projection matrix and $A_{ij}(t)$ gives the per capita rate at which individuals in stage j at time t contribute to or become individuals in stage i at time $t+1$. (Note: for all projection matrices, we follow the column to row ($j \rightarrow i$) parametrization). Transition probabilities and reproductive rates are estimated from field data on marked individuals. In a variable environment, at each time step, the environmental state determines demographic rates; the matrix $\mathbf{A}(t)$ takes on values $\mathbf{A}_1, \mathbf{A}_2, \dots, \mathbf{A}_K$, where K is the number of environmental states. We assume that environmental transitions follow a Markov chain with a transition matrix $\mathbf{T} = (T_{\alpha\beta})$, for environments $\alpha, \beta = 1, \dots, K$ (transitions are $\beta \rightarrow \alpha$). Each population experiences some random sequence of environmental states (sample path, ω) over time, each state comprising proportion π_β of the stationary distribution. The total population $P(t)$ at time t is the sum of the elements of $\mathbf{N}(t)$ and the stochastic growth rate, λ_S , is obtained from

$$\log \lambda_S = \lim_{t \rightarrow \infty} (1/t) \log (P(t)/P(0)) \quad (1)$$

As in deterministic population dynamics, stochastic population growth rate and its sensitivities (including elasticity) are defined asymptotically. As in deterministic population dynamics, the long-run stochastic dynamics are ergodic (under similar assumptions as the deterministic), such that the population eventually follows a stationary dynamic distribution of structures that is independent of initial environment and initial stage structure (Tuljapurkar 1990).

Methods: Environment-specific elasticity

Stochastic elasticity, an analogue of deterministic elasticity and the ij^{th} element of $\mathbf{E}^S$, written e_{ij} , is the proportional change in λ_S produced by a 1 % change in the ij^{th} population matrix element in *every* state of the environment. However λ_S may respond differently to perturbations of life history rates in *particular* states of the environment. The latter responses are described by matrices of environment-specific elasticities $\mathbf{E}_\beta^S$. The entry, $e_{i,j,\beta}$ in each matrix is the % change in λ_S produced by a 1% change in the ij^{th} life history transition rate when the population is in environmental state β . We previously used the term “habitat-stage” elasticity (Horvitz et al. 2005), but here adopt the more intuitive term “environment-specific” elasticity, proposed by Caswell 2005 in an independent derivation of the same idea. We have shown (Horvitz et al. 2005) that $e_{i,j,\beta}$'s are determined by the

(expected) “future” sequence of environmental states, which depends upon, and differs according to, the current state β . Each $e_{i,j,\beta}$ value also includes a weighting that depends upon how frequently the β state occurs. To unweight it and focus on the “distilled” expected sequence effect, we determine the ‘per-occurrence’ normalized environment-specific elasticity, which is just $e_{i,j,\beta}$ divided by the frequency of state π_β in the long-run sequence (Horvitz et al. 2005). These are readily calculated by numerical simulation (Horvitz et al. 2005, 2010). The calculations that estimate the asymptotic long-run stochastic growth rate and its sensitivities are performed after discarding the transients.

Methods: Environment-specific selection gradients

Each matrix element affected by the trait of interest is a fitness component. Consider the $N(t, j)$ of individuals (with individual trait values $z_1, z_2, \dots$) in stage j when the environment is in state β . The value of $a_{i,j,\beta}$ is the ratio of the total number of individuals in stage i at $t + 1$ produced by individuals who were in stage j , to the number $N(t, j)$. For every individual in stage j , there is an individual transition rate to every possible final stage i . When i is the stage for newborn offspring alive at $t + 1$, the individual rate for the transition from j to 1 is the number of newborn offspring produced by that individual who are counted at $t + 1$. When i is any other stage, the individual transition rate is 0 or 1. Thus an individual whose trait value is z has individual transition rates $a(i, j, \beta, z)$, and $a(i, j, \beta)$ is the mean of these individual rates over all trait values. If we regress the mean-standardized fitness components, $[a(i, j, \beta, z)/a(i, j, \beta)]$ against the mean-standardized trait values $z/\bar{z}$ (as in van Tienderen 2000 and Coulson et al. 2003), the regression coefficient $s_{i,j,\beta}$ is analogous to a mean-standardized selection gradient in an unstructured population, which measures the “increase in relative fitness (component) for a proportional change in the trait z ” (Hereford et al. 2004). (An unstructured population is defined by the total number of individuals rather than by the number of individuals in each of several different stages or ages.) Mean standardized selection differentials are not based on any particular assumptions about the distribution of the trait or of the fitness component. In addition, the quantity $s_{i,j,\beta}$ is an estimate of the derivative

$$\frac{\partial \log a(i, j, \beta)}{\partial \log \bar{z}}.$$

We define a matrix of regression coefficients $\mathbf{S}_\beta$ in each of the K states of the environment, for a total of K such matrices.

The regressions should ideally be estimated using the same group of individuals for which the matrix element is calculated, the individuals in stage j at time t , but in practice the regression relationships are often calculated for a different set of individuals in the same population, as long as they are in the same time period, stage and population.

Methods: Integrated selection in the variable environment

Our fitness measure is the stochastic growth rate λ_S (Tuljapurkar 1982b, 1990) and we are interested in the change in fitness resulting from a change in the mean trait value $\bar{z}$. We have

$$\begin{aligned}\frac{\partial \log \lambda_S}{\partial \log \bar{z}} &= \sum_{\beta} \pi_{\beta} \sum_{ij} \left(\frac{\partial \log \lambda_S}{\partial \log a(i,j,\beta)} \right) \left(\frac{\partial \log a(i,j,\beta)}{\partial \log \bar{z}} \right), \\ &= \sum_{\beta} \pi_{\beta} \sum_{ij} e_{i,j,\beta} s_{i,j,\beta}.\end{aligned}\quad (2)$$

The right hand side sums over environments and over all matrix elements (i.e., fitness components) of the product of the elasticities $e_{i,j,\beta}$ and the mean-standardized selection gradients $s_{i,j,\beta}$ as indicated in the last line above.

It is useful to define a matrix of integrated selection values

$$\mathbf{M}_{\beta} = \mathbf{S}_{\beta} \circ \mathbf{E}_{\beta}. \quad (3)$$

for each state of the environment β which is the element-wise product of environment-specific regressions with environment-specific elasticities. There are a total of K such matrices. We propose that an entry, $m_{i,j,\beta}$, measures how the stochastic growth rate λ_S would be affected by a proportional change in demographic rates brought about by a proportional change in a trait value in environment β . If we were to apply a terminology parallel to van Tienderen (2000), these would be called the “environment-specific elasticities of a trait.” We prefer to call the $m_{i,j,\beta}$ components of “total integrated selection,” since our goal is to measure selection in the context of natural patterns of demographic and environmental variation. By “total integrated selection” we mean the total selection on a trait in the random environment obtained by summing $m_{i,j,\beta}$ over all life history transitions in all environmental states, over all i, j and β . Sums of the $m_{i,j,\beta}$ over appropriate subsets of transitions and/or environments measure the relative contributions of different life history pathways or of different environments to total integrated selection.

Total integrated selection is a prospective measure: it predicts the proportion by which the mean trait value would change on average per year in the stochastic environment over the long run, given a set of demographic matrices, a set of mean-standardized selection gradient matrices and a particular model of environmental dynamics. Our integrated measure describes the force of selection, not the genotypic response to selection. To describe the latter, one would need data about the genotype-phenotype map and the distribution of genotypes. Our analysis focuses on single traits rather than multiple correlated traits.

A heuristic approach to describing the genetic response to selection can be made by following the theory developed for structured populations in deterministic environments by Charlesworth (1974, 1980, 1993, 1994) and Lande (1982). Assuming that (i) there is no density-dependence, Charlesworth (1980, 1994) showed that fitness is the Lotka growth rate r . If we further assume that (ii) genotypes are determined by alleles at a single locus in a diploid randomly mating population, (iii) a phenotypic trait z is additively determined by alleles at many unlinked loci and (iv) the mean trait value equals the mean breeding value, Charlesworth (1993) showed that the dynamics of the population mean trait value $\bar{z}$ are described by the equation

$$\frac{d\bar{z}}{dt} = G \left(\frac{dr}{d\bar{z}} \right),$$

where G is the additive-genetic variance in the trait. Lande (1982) originally derived this result by assuming normal distributions of phenotypes and fitness but Charlesworth showed that we need only make assumptions (i) to (iv) above. It is important to stress that G depends on the state of the population and that it changes over time. Hereford et al. (2004) pointed out that Lande's original equation gives the unstandardized response to selection as a product of additive genetic variance (σ_A^2) with the unstandardized selection gradient (1979), while the σ -standardized response to selection is a product of heritability with the σ -standardized selection gradient (Lande and Arnold 1983). However, mean-standardized response to selection is a product of I_A (the square of the coefficient of variation of the additive genetic variation, $CV_A = \sigma_A/\bar{z}$) with the mean-standardized selection gradient (Houle 1992).

It has been shown that a replaces r under assumption (i) in a stochastic environment (Tuljapurkar 1982b). It is therefore plausible that under assumptions (ii) to (iv), r will continue to be replaced by a in a stochastic environment. However, in a stochastic environment, it is the mean trait value $\bar{z}$ that follows a stochastic process, so the deterministic Lande result will be replaced by an equation for the rate of change of the (stochastic) average $\bar{z}$. This argument has been carried through and the dynamics have been found to follow a diffusion (proof in S. Tuljapurkar and T. Coulson, unpublished ms). These heuristical arguments make it plausible that the stochastic generalization of Lande's deterministic result is

$$\frac{d\bar{z}}{dt} = I_A \sum_{\beta} \pi_{\beta} e_{i,j,\beta} s_{i,j,\beta}. \quad (4)$$

Methods: Data requirements

Two kinds of population-level data are needed to apply this method. First, individual trait values z and individual fitness measures w (e.g., binomial survival, multinomial stage transition rates, and number of offspring produced) are estimated for individuals in given environments. Individuals are grouped by stages in each state of the environment for regression analysis of fitness components vs. trait values. Second, mean demographic rates for individuals grouped by stages within each environment are used to construct population projection matrices. Below are two useful examples where both types of data were available, one is a plant study and the other an animal study, but they each contain elements of general interest. Both studies were interested in understanding selection in variable environments. In our examples, matrix elements were either proportional to the measured fitness components or identical to them. In other examples, matrix elements may be constructed from products of measured fitness components and the chain rule would apply.

Also required is data at the environment level to parameterize a model of environmental dynamics that provides the probability rules which generate the stochastic sequence of environments. This type of data is rarely known, but the results we present here indicate that it should be sought. For each of our examples, we illustrate two possible temporal patterns, one generated by long term climate data and a second generated by a distinct model of environmental dynamics (e.g., an assumption that environments usually do not change, or an assumption that an observed long-term sequence is the most likely pattern). Our method makes use of data from observed single-year transitions and selection, but produces expected long-term demographic and selective responses. We show that the expected strength of selection depends upon temporal patterning in the environment.

Results

Example 1. *Calathea ovandensis* (Marantaceae)

Demography—This species is a perennial forest herb that inhabits a seasonal tropical forest in the Los Tuxtlas region of Veracruz, Mexico. Eight stages characterize the population vector: seeds (both newly produced and those in the seed bank), seven other size classes (three non-reproductive and four reproductive). Seed production increases with plant size because the number of reproductive shoots increases (not the seed production per shoot). During the dry season, plants lose all above-ground biomass and seeds are dormant. Both germination and vegetative growth begin each year with the onset of the rainy season; flowering and fruiting occur later in the wet season. The annual demographic census occurs when seeds are readily counted in mature fruits on plants. Plants that are non-reproductive in year t can become reproductive by $t + 1$ and thus contribute to seeds at $t + 1$ (Horvitz and Schemske 1995). For this paper, we pooled data among four study sites located within the same forest to construct annual population projection matrices for each of four transition years. The years differed in several demographic rates including seed production per reproductive shoot (Figure 1A) and germination rate, resulting in inter-annual variation in overall demographic quality as measured by the dominant eigenvalue of that year's matrix (Figure 2A). We considered these matrices to represent potentially four states of the demographic environment.

Mean-standardized environment-specific selection gradients—Here we focus on floral tube length, a trait that mediates the nature of the interaction between insect visitors and the plant. The match between insect tongue length and floral tube length determines the outcome of visits to these rather unusual flowers in which the reproductive parts are not exposed unless the flower is “tripped” and only the particular visit that “trips” the mechanism can result in pollination. Insect visitors with short tongues have to insert their heads deeper into flowers to be able to reach the nectar, resulting in higher per-visit tripping- and pollination- efficiency. In contrast, visitors with long tongues rarely trip the mechanism (Schemske and Horvitz 1984). In a three year study, Schemske and Horvitz (1989) found annual variation in relative abundances of insect visitors and in selection on floral tube length.

In the 1989 paper, selection was measured by regressing relative fitness, measured as fruit production per inflorescence, against floral tube length. In the year when the shortest-tongued visitors had the highest relative abundance there was significant negative directional selection on tube length, i.e. plants with the shortest tubes produced the most fruits. To be able to use these data for the current analysis, we recalculated the regression relationships for each of the three years of data, regressing relative fruit production against mean-standardized floral tube length (regression parameters in Figure 1B). Mean-standardized stage-specific selection gradients varied among years and could be quite strong, ranging from -6.9 to $+3.1$; in this example, selection acts through reproduction only (Figure 1B). We consider these to represent three states of the selective environment for floral tube length. We matched them up to their respective chronological counterparts of the demographic study. For the first year of the demographic study, there was no study of selection. For purpose of example, we assign it the same selective environment as the year with the highest relative abundance of short-tongued pollinators.

Climate variable of interest—The severity and duration of the dry season in seasonal tropical climates is an environmental parameter of interest. In particular, for our study organism, it influences how soon plants and seeds emerge from dormancy once the rains begin (C.C. Horvitz and D.W. Schemske, unpublished data). We obtained long term climatological records for the nearby town of San Andres Tuxtla (Veracruz) from the Servicio Nacional de Meteorología of Mexico, and calculated the average-monthly-dry season-rainfall (using the months Nov–May) for each year. Here, “year” refers to the interval that corresponds to our demographic census interval (Aug to Aug). We calculated the mean and standard deviation of this average-monthly-dry-season-rainfall over all the years in the historical record ($N = 57$, 1926–27 to 1987–88, five years in mid 1930’s missing) and estimated $\mu = 57.4$ mm, $\sigma = 25.2$ mm. We determined how much each year deviated from the mean in standard deviation units. To determine environmental dynamics, we defined five categories of dry season rainfall from “very dry,” a year with rainfall > 1.5 standard deviation units below the mean to “very wet,” a year with rainfall > 1.5 standard deviation units above the mean. “Mean” was a year with rainfall value ± 0.5 standard deviation units from the mean. Intermediate categories, “wet” and “dry,” were for years with rainfall > 0.5 units but < 1.5 units away from the mean. In the 57 years of climate data there were 3 and 4 years respectively in the extreme categories “very dry” and “very wet” and 20 years in the “mean” category. Our demography study encompassed one representative year each from the following climate categories: dry, wet, mean, very wet (Figure 3A).

To facilitate matching our demographic data to the historical climate record, we combined the “very dry” and “dry” categories of the historical record into one, renamed “dry.” We then used the historical climate record to create a Markov chain model of the environment (illustrated in Appendix 1A), where the environmental state was one of the four categories; we simply counted the number of times each given state either stayed the same or transitioned to any other state over one time step. The model generated a stochastic sequence (100,000 time steps) of environments, corresponding to a stochastic sequence of demographic matrices and selection gradient matrices from which we calculated the stochastic growth rate, its elasticities and the new measure of integrated selection.

One alternative environmental driver—As an alternative way to dynamically combine our observations over time, we employed a Markov chain model in which the most likely outcome was environmental stasis (illustrated in Appendix 1B). The goal of this was not so much to propose that one is more correct for the study organism than the other as it is to explore how environmental dynamics may influence the strength, direction and pathway of selection. This model generated a distinct stochastic sequence (100,000 time steps) of environments, corresponding to a stochastic sequence of demographic matrices and selection gradient matrices from which we calculated the stochastic growth rate, its elasticities and the new measure of integrated selection.

Environment-specific elasticity—One component of environment-specific elasticity contains information about the expected frequency of each environment. Under the climate-based driver of environmental change, environment 1 is the most frequent ($\pi_1 = 0.34$) in the stochastic sequence and environment 4 the least frequent ($\pi_4 = 0.07$) (Table 1). The stasis-based driver of environmental change (in which environments have high probability of remaining the same), results in an opposite pattern, with environment 4 being the most frequent ($\pi_4 = 0.33$) and environment 1 least frequent ($\pi_1 = 0.17$). The predominance of environment 4 emerged because of the particular rules we used in the Markov process; when environments did change, it was more often the case that they changed to environment 4 than to environment 1 (Appendix 1B).

The other component of environment-specific elasticity contains information about the dependency of environment-specific elasticity on the sequence in which a given environment is most often embedded. Here we consider only those population projection matrix elements for which there is corresponding selection gradient data, in this case the contributions to next year's seeds by juveniles, pre-reproductives and four size classes of reproductives. For the climate-based driver of environmental change, this component was quite similar among the different environments (Figure 4A), meaning that the sequence of environments in which a given environment is embedded was relatively independent of current environmental state. The stochastic growth rate was $\lambda_S = 0.9888$ (Table 2); it is most elastic to seed production by small reproductives, very slightly more so when the population is in environment 3 (Figure 4A). For the stasis-based driver of environmental change, this component of environment-specific elasticity varies more among environments (Figure 4B), meaning that the sequence of environments in which a given environment is embedded is more dependent upon current environmental state. The stochastic growth rate was $\lambda_S = 0.9867$ (Table 2); it is most elastic to seed production by small reproductives as in the previous driver, however, in contrast, in two environments it is also highly elastic to seed production by the largest reproductives; and it is more elastic to reproduction by plants when they are in environments 1 and 4, rather than environment 3 (Figure 4B).

Integrated selection—For the climate-based driver of environmental change, selection on floral tube length (normalized by the frequency of the environmental state) is influenced much more by future seed production of small reproductives than reproduction of any other stage class (Figure 4C). There is a strong signal of the stage-specific normalized selection gradients (Figure 1B) since environmental differences in environment-specific elasticity are

minimal (Figure 4A). Selection for shorter tubes occurs each time the environment is in state 1 or 3, while selection for longer tubes occurs each time the environment is in states 2 or 4 (Figure 4C). Summing up across the entire sequence of environments, we find selection for shorter floral tubes dominates; total integrated selection $m_{i,j,\beta}$ summed over stage and environment is -0.1731 (Table 2). Most of this total comes from selection through reproduction of small reproductives (Figure 7A), summed across all environments. Summing across all contributions of all stages reveals that selection for shorter tubes in environments 1 and 3 outweighs selection for longer tubes in environments 2 and 4 (Figure 8A).

For the alternate driver of environmental change, based on environmental stasis, the picture of selection on floral tube length (normalized by the frequency of the environmental state) is similar, but much less concentrated in small reproductives (Figure 4D). The signal of the stage-specific normalized selection gradients (Figure 1B) is less dominant since there is more environmental difference in environment-specific elasticity (Figure 4B). Summing up across the entire sequence of environments, we find that selection for shorter floral tubes still dominates, but not quite as much as above; total integrated selection $m_{i,j,\beta}$ summed over stage and environment is -0.1083 (Table 2). This total is not as dominated by small reproductives; other reproductive and pre-reproductive stages contribute a bit more (Figure 7B), summed across all environments. Summing across all contributions of all stages reveals that selection for shorter tubes in environments 1 and 3 still outweighs selection for longer tubes in environments 2 and 4, although the contributions of the different states of the environment to total selection are more similar (Figure 8B).

Example 2. *Cervus elaphus*, Red Deer

Demography—We used data from a population of red deer living in the North Block of Rum, Scotland. This is a unique data set that provides an exceptional opportunity to highlight the ways to incorporate temporal variation in demography and selection. Although to our knowledge, no comparable data for plants are available yet, we hope that this example inspires their future availability. Life history data on uniquely marked individuals of this population have been collected since 1971. Twenty age-sex categories have been used to structure annual demographic rates based on a parsimony analysis of mark-recapture data. On this basis, females are divided into eleven stages (yearlings, prime adults aged 2, 3, 4, ..., 10, and older adults aged 11 and more) and males are divided into nine stages (yearlings, prime adults aged 2, 3, 4, ..., 8, and older adults aged 9 or more). In this paper we focus on the dynamics of the females, modelled by an 11×11 population projection matrix and we assume the survival rate of prime adult females is equal to that of older adult females. Births occur in late May to June and calves are weaned by October. Mating takes place in late September to October. The population is food limited during the winter and most mortality occurs between January and April. The annual census interval for the model we use here begins in mid-May; this is a pre-breeding census and recruitment rate per adult female is calculated as number of female calves born to each female $\times$ neonatal survival [birth to October] $\times$ their winter survival [October to mid-May] to the following May (as in Coulson et al. 2003). For this paper, annual population projection matrices were constructed for each of 26 transition years from 1975–1976 to 2000–2001, hereafter designated as the “1975,”

“1976,” ..., “2000” years. The years differed in demographic rates (recruitment, yearling survival and prime survival) (Figure 1C–E), resulting in inter-annual variation in overall demographic quality as measured by the dominant eigenvalue of each year’s matrix (Figure 2B). We considered these matrices to represent potentially 26 different states of the demographic environment.

Mean-standardized environment-specific selection gradients—Here we focus on the time of birth (counted as days after January 1); selection on this trait varies across years. When there is a mild spring, an early birth is expected to be advantageous while in years with a harsh spring, an early birth would likely be disadvantageous. A mild spring gives an early calf a longer growing season, thus a greater chance to get established before the first winter, an advantage which may in turn influence an individual’s future survival and eventual reproductive output. Thus the time of birth is a neonatal trait that may influence fitness components throughout the life of individuals. Selection was measured by regressing relative fitness, measured as that year’s production of recruits or that year’s survival, against mean-standardized time of birth; for the latter logistic regression was employed (Coulson et al. 2003)(regression parameters in Figure 1F–H). We consider these to represent 26 states of the selective environment for the quantitative trait, time of birth (counted as days after January 1). We matched them up to their respective chronological counterparts of the demographic study. Mean-standardized stage-specific selection gradients varied among years and could be quite strong, ranging from -6.8 to $+4.9$ for selection through reproduction (Figure 1F); from -2.9 to $+1.6$ for selection through female yearling survival (Figure 1G); and from -0.8 to $+0.17$ for selection through female prime survival (Figure 1H).

Climate variable of interest—The winter North Atlantic Oscillation Index (NAO), which is measured between Iceland and Lisbon, impacts the winter climate of the study region. When the NAO Index is negative, the winter is colder and when it is positive the winter is warmer, but wetter and stormier at the study site. We used the annual NAO indices from 1864–2006, which ranged from -4.6 to $+4.9$, (Hurrell 1995), to calculate a mean and standard deviation ($N = 143$ yrs, 1864–2006, none missing), $\mu = 0.17$, $\sigma = 1.91$. We determined how much each year deviated from the mean in standard deviation units. To determine environmental dynamics, we defined ten categories, from > 2.5 standard deviation units less than mean to > 2.0 standard deviation units above the mean. Intermediate categories were delimited by 0.5 units, with the sixth category including the mean and ± 0.5 sd units above or below it. In the 143 years of climate data, there was only 1 year each belonging to the two extremes categories (one or ten) and 51 years belonging to the mean category (six)(Figure 3B). We used the historical climate record to create a Markov chain model of the environment, where the environmental state was one of the ten NAO index categories; we simply counted the number of times each given state either stayed the same or transitioned to any other state over one time step. The model was used to generate a stochastic sequence (100,000 time steps) of environments, where environments are any of the ten states.

We next translated this sequence into a sequence involving the 26 environmental states represented by our 26 demographic matrices. First, we associated a set of demographic rates with each NAO index category, matching the annual value of the NAO index to demographic transition years of the deer study, as follows. The 1976 NAO index was measured between Dec 1975–Mar 1976 and thus corresponds to the 1975–1976 demographic transition year for the deer, which we call the “1975” year. Of our 26 years of demographic data, 10 of them were from years with an intermediate NAO index (the sixth category), 4 from years with relatively low NAO indices (the first to fifth categories) and 12 for years with relatively high NAO indices (the sixth to tenth categories) (Figure 4B). For NAO index categories with no matching data, we assigned the data that corresponded to the next highest category; for NAO index categories with several possible data matches, we drew from the possibilities at random with equal probability. This protocol allowed us to translate the stochastic sequence of NAO index categories into a stochastic sequence (100,000 time steps) of the 26 environmental states represented in our demographic data, corresponding to a stochastic sequence of demographic matrices and selection gradient matrices from which we calculated the stochastic growth rate, its elasticities and the new measure of integrated selection. A Markov model chain constructed from this sequence is illustrated in Appendix 1C.

One alternative environmental driver—As an alternative way to dynamically combine our observations over time, we considered a Markov chain model in which the most likely outcome was the actual observed sequence of the 26 environments (illustrated in Appendix 1D). The goal of this is not so much to propose that one is more correct for the study organism than the other as it is to explore how environmental dynamics may influence the strength, direction and pathway of selection. This model generated a distinct stochastic sequence (100,000 time steps) of the 26 environmental states represented in our demographic data, corresponding to a stochastic sequence of demographic matrices and selection gradient matrices from which we calculated the stochastic growth rate, its elasticities and the new measure of integrated selection.

Environment-specific elasticity—One component of environment-specific elasticity contains information about the expected frequency of each environment. Under the climate-based driver of environmental change, environment 3, corresponding to a year for which the NAO index was close to its mean (Figure 3B), was the most frequent ($\pi_3 = 0.0568$) in the stochastic sequence; while, environment 14, corresponding to a year for which the NAO index was 2.5 standard deviations above its mean, was the least frequent ($\pi_{14} = 0.0071$) (Table 1). The “26-yr cycle” driver of environmental change (in which environments 1 through 25 were assigned a high probability of becoming the environment that was observed to come next (2 through 26, respectively) and the 26th environment was assigned a high probability of returning to environment 1), resulted in a pattern in which all environments were equally frequent ($\pi_\beta = 0.0385$, for all β).

The other component of environment-specific elasticity contains information about the dependency of environment-specific elasticity on the sequence in which a given environment is most often embedded. Here we consider only those population projection

matrix elements for which there is corresponding selection gradient data, in this case, recruitment of new females (top row of the matrix, columns 3 through 11), female yearling survival (row 2, column 1), female prime survival (subdiagonal elements of columns 2, 3, ..., 10 and the diagonal element of column 11).

Considering the climate-based driver of environmental change first, the stochastic growth rate was $\lambda_S = 1.0275$ (Table 2). It is about $4 \times$ more elastic to survival than to recruitment (Figure 5A and 5B). It is quite elastic to recruitment by 3-yr olds, the youngest reproductives. It is generally less elastic to recruitment by older females than by younger females, although it is most elastic to the “> 10 yrs old” category (which has very high stasis since it accumulates all the older individuals into one class). Normalized recruitment elasticity is generally more similar among the environments for older age classes than for younger age classes, although for both the 3-yr olds and the “> 10 yrs old” category, it is quite variable among environments (Figure 5A). The stochastic growth rate is most elastic to survival of yearlings and two-year olds, and is generally less elastic to survival of older females. Normalized survival elasticity is quite similar among the environments for most age classes, except, for the “> 10 yrs old” category (Figure 5B).

For “26-year cycle,” the alternative driver of environmental change, the stochastic growth rate was $\lambda_S = 1.017$ (Table 2). It was also about 4-fold more elastic to survival than to recruitment (Figure 5C and 5D), similar to above, although the effects of environment for the elasticity parameters differ in shape between the two environmental drivers (Figure 5A vs Figure 5C and Figure 5B vs Figure 5D). For example, examine the lines for the elasticity of stochastic growth rate to recruitment by the “> 10 yrs old” category; the locations of peaks and valleys as well as the magnitude of the fluctuations differ. What is similar is that generally the stochastic growth rate is less elastic to recruitment by older females than by younger females, as above, but there is much less distinction among ages and more variability for a given age among environments than in the climate-driven scenario. It remains most elastic to recruitment by females in the “> 10 yrs old” category (which has very high stasis since it accumulates all the older individuals into one class) (Figure 7C). The picture of elasticity to survival is especially distinct, with very large variation among environments for a given age class and a clear cycling across ages and environments (Figure 5D).

Integrated selection—For both drivers of environmental change, variation among environments in their contributions to integrated selection on time of birth (normalized by the frequency of environmental states) bears the strong signal of the stage-specific selection gradients (compare Figure 1F–H and Figure 6). In particular, integrated selection acting through recruitment by females of all ages exhibit peaks (selection for later birth) and valleys (selection for earlier birth) in the same environmental states (Figure 1F). The strongest selective pressure (acting through recruitment) to be born later in the season occurs every time the environment is in states 3 or 26, while the strongest selective pressure to be born earlier in the season (acting through recruitment) occurs when the environment is in state 25 (Figure 6A, 6C). The relative magnitudes of selection at each peak and valley, which indicate the relative contribution to total selection, depend upon age class, with the “> 10 yrs old” category contributing the most. The degree to which the remaining age classes

vary in their contributions to overall selection through recruitment is only slightly different between the climate-driven scenario and the alternate “26-yr cycle” scenario (Figure 6A, 6C), resulting mostly from subtle differences in the normalized environment-specific elasticity (Figure 5A, 5C).

In general there is stronger integrated selection through survival of yearlings than through survival of prime females (Figure 6B, D). Integrated selection acting through survival bears distinct signatures for yearlings vs prime females (Figure 6B, D) similar to their distinct patterns of stage-specific selection gradients (Figure 1, G and H, respectively). For yearling survival, the strongest selective pressure to be born later in the year occurs each time the environment is in state 10, 18 and 21 and the strongest selection pressure for earlier birth occurs each time the environment is in state 6, 7, 8 or 19; while for prime survival there is very limited selection for later birth, and notable selection for earlier birth each time the environment is in state 5, 18 or 25.

Summing up across the entire sequence of environments, we find selection for earlier birth dominates; total integrated selection $m_{i,j,\beta}$ summed over stage and environment is -0.2471 for the climate-driven scenario and -0.2892 for the alternate “26-yr cycle” scenario (Table 2). This total comes from selection through both recruitment and survival summed across all environments, with selection through recruitment making a relatively larger contribution to the total and recruitment by females in the “> 10 yrs old” class dominating (Figure 7C, D). For the other age classes, the contribution to selection through recruitment declines with age. Similarly, the contribution to selection through survival generally declines with age. The “26-yr cycle” scenario indicates a dominant contribution by yearling survival to the total selection (Figure 7D) that is not seen in the climate-driven scenario (Figure 7C). Summing across all contributions of all stages reveals that selection for earlier birth in most environments far outweighs selection for later birth seen in environments 5 and 26, principally and, in 21, 17, 17 and 10, in small measure (Figure 8C, D).

Discussion

The study of natural selection is central to understanding the rates and mechanisms of adaptive evolution. One key issue concerns the strength of selection in nature—is selection typically weak, as might be expected if populations are near a phenotypic optimum for a given environment, or instead, is selection strong, as would be expected for populations experiencing novel environmental conditions? Three reviews of the published literature have addressed this question. Kingsolver et al. (2001) concluded that directional selection was typically weak, although the frequency distribution of selection gradients displayed a long right tail, indicating that selection was sometimes strong. In contrast, Hereford et al. (2004) concluded that selection in nature was typically strong. The marked difference in the conclusions of these two studies is probably due, at least in part, to the different metrics employed to estimate selection strength. While Kingsolver et al. (2004) used variance-standardized measures of selection; Hereford et al. (2004) used mean-standardized selection gradients. In their review of temporal variation in selection strength, Siepielski et al. (2009) used variance-standardized selection gradients and concluded (p. 1268) that most

populations "... experience infrequent bouts of strong selection, tempered with other bouts of weaker selection."

These results must be interpreted with caution. To obtain an accurate estimate of selection strength requires integrating measures of selection derived from the study of traits with the study of the contributions of those traits to fitness. For this purpose, fitness is best defined in demographic terms, as the net effects of growth, survival and reproduction (Lande 1982). As emphasized by Caswell (2001, p. 280), "... selection must be studied in terms of the entire life cycle. The alternative –analysis in terms of a subset of the vital rates, or what are called components of fitness– risks getting answers that are qualitatively wrong." Most of the studies included in the reviews discussed above examined only a subset of the life history, thus we cannot know how their findings might change if overall fitness had been used to estimate selection strength.

Taken together, the reviews of selection strength (see above) establish the need for long term data on selection in wild populations. In addition, they point to the need for development of new conceptual tools that can make effective use of such data to integrate total selection (which may change in sign and magnitude) over life history and across temporally variable environments. We have provided one such new approach in this paper that may be useful especially for organisms with structured populations (in which growth, survival and reproduction vary with age or stage and dynamics are modelled by projection matrices) when selection is variable but relatively weak. Leaving formal mathematical arguments for a later paper, here we proposed a way to think about this problem and demonstrated the implementation of the method. In brief, to estimate total integrated selection on mean trait value over stages and environments, (1) for each matrix element (fitness component) in each state of the environment determine the regression relationship between the trait and the individual matrix element; (2) multiply these environment-specific, stage-specific regression coefficients by environment-specific, stage-specific elasticities of the stochastic growth rate; and (3) sum over all relevant life history and environmental paths.

This approach provides an estimate of the strength of selection integrated over several components of the life cycle and several variants of the environment. Such an integrative measure can not be obtained from studies of subsets of components of fitness without regard to temporal fluctuations. In light of this backdrop, we next examine the insights derived from applying our approach to the two study systems described above.

Perspectives on selection studies of *Calathea*

In studying floral tube length in *Calathea*, Schemske and Horvitz (1989) did not previously estimate mean-standardized selection gradients and did not previously integrate over life history paths. They calculated univariate variance-standardized selection gradients (which they called i , although what they calculated is the same as what Kingsolver et al. [2001] call β and Hereford et al. [2004] call β_{σ}) for selection acting through reproduction. Values across three years ranged from -0.26 standard deviation units to $+0.08$ standard deviation units. For the current paper, we used the same data to calculate mean-standardized selection gradients for each of the 3 years, resulting in values ranging from -6.898 to $+0.300$, with an average over the 3 years of -1.362 . Using this average, we might expect that for a 1% increase in

mean corolla we would expect about 1.4% decrease in relative fitness as measured by fruit production. If we used the environmental weightings given by the stationary distribution of the stochastic sequences generated by the models of environmental change proposed in this paper, we would predict much larger changes, with means of -3.233 and -2.518 for the dry season rainfall and environmental constancy models, respectively.

However, such simple weighted averages do not take into account either the dynamics of the system or the low elasticity of total fitness to reproduction. The new measure of integrated selection does and it predicts a much smaller change, of only 0.1% to 0.2% decrease in relative fitness, now measured by λ_S , for each 1% increase in mean corolla. Decomposition of the total integrated selection into various sums provides unique insights; for example selection acts more through small reproductives (stage 5) than the through the other stages even though they do not have the highest seed production. Also, it is worth noting that although the two models of environmental dynamics result in very similar population growth rates, they differ substantially in the total integrated selection on floral tubes, which is $1.7 \times$ stronger for the model based on climate than for the alternative model. The relative contribution of different stages and the relative contribution of different environmental states to total selection differs between these models.

Perspectives on selection studies of Red Deer

In studying neonatal traits of Red Deer, including timing of birth, Coulson et al. (2003) previously estimated mean-standardized stage-specific selection gradients. As we have seen here, they were quite variable and sometimes quite strong, ranging to -6.8 for selection through reproduction, -2.9 for selection female yearling survival and $+0.8$ for selection through female prime survival. Coulson et al. also previously integrated over all these different pathways of selection and included weightings by elasticities of λ to the different life-history rates, doing it year by year (or over other fixed time periods), following van Tienderen (2000). The mean selection on birth date from their analyses over the same 26 year period as the current paper was -0.229 . This is a figure similar to the values obtained here using the new measure of integrated selection, which predicts a decrease of 0.2% to 0.3% in relative fitness for each 1% increase in mean time of birth, depending on the model of environmental change.

Nevertheless, Coulson's previous analysis did not take into account the dynamics of the environment *per se*. The new measure of integrated selection provides significant refinements and advances understanding. Total integrated selection varied with the model of environmental dynamics; it was $1.2 \times$ stronger in the environment that followed the observed sequence of environments than it was in the climate-driven model. As well, selection acted through the survival of yearlings much more so in this model, emphasizing the general result that the demographic rate via which selection operates varies with environmental sequence, *i.e.* the future matters. Finally, it is somewhat surprising that despite a large difference between the stationary distributions of environments associated with each of the two models, the relative contributions of environments to selection was strikingly similar between them, with only subtle differences.

Conclusions

Temporal patterning in the environment has selective consequences. Linking models of environmental change to relevant short term data on demography and selection may permit estimation of the strength of selection over the long-term in variable environments. Building models that can extend necessarily time-limited studies to long-term contexts is important. To understand selection in temporally variable environments one needs to work through all components of fitness. Just working with single components of fitness is likely to give misleading results. Such a rich picture of the role of environmental variation on selection could not be obtained with measures of fitness like lifetime reproductive success. Linking stochastic demography to selection gradients offers great potential to help forge links between two somewhat disparate fields. The method we have presented could, in concept, be extended to multiple correlated traits. Whether selection measured in this way is typically weaker, stronger or different in sign than that measured by single component fitness at one point in time awaits future studies.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Literature Cited

- Aberg P, Svensson CJ, Caswell H, Paviac H. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. *Ecological Modelling*. 2009; 220:605–610.
- Arnold SJ, Wade MJ. On the measurement of natural and sexual selection: applications. *Evolution*. 1984a; 38:720–734.
- Arnold SJ, Wade MJ. On the measurement of natural and sexual selection: theory. *Evolution*. 1984b; 38:709–719.
- Caswell, H. Matrix population models: construction, analysis and interpretation. 2. Sinauer Associates; Sunderland, Massachusetts, USA: 2001.
- Caswell H. Sensitivity analysis of the stochastic growth rate: three extensions. *Australia and New Zealand Journal of Statistics*. 2005; 47:7585.
- Caswell H, Trevisan MC. The sensitivity analysis of periodic matrix models. *Ecology*. 1994; 75:1299–1303.
- Charlesworth B. Selection in populations with overlapping generations VI. Rates of change of gene frequency and population growth rate. *Theoretical Population Biology*. 1974; 6:108–133. [PubMed: 4418568]
- Charlesworth, B. *Evolution in Age-structured Populations*. Cambridge: Cambridge University Press; 1980.
- Charlesworth B. Natural-Selection on Multivariate Traits in Age-Structured Populations. *Proceedings of the Royal Society of London Series B-Biological Sciences*. 1993; 251:47–52.
- Charlesworth, B. *Evolution in Age-structured Populations*. 2. Cambridge: Cambridge University Press; 1994.

- Coulson T, Kruuk L, Tavecchia G, Pemberton J, Clutton-Brock T. Estimating selection on neonatal traits in red deer using elasticity path analysis. *Evolution*. 2003; 57:2879–2892. [PubMed: 14761065]
- Coulson T, Tuljapurkar S. The dynamics of a quantitative trait in an age-structured population living in a variable environment. *American Naturalist*. 2008; 172:599–612.
- Haridas CV, Tuljapurkar S. Elasticities in variable environments: properties and implications. *American Naturalist*. 2005; 166:481–495.
- Hereford J, Hansen TF, Houle D. Comparing strengths of directional selection: how strong is strong? *Evolution*. 2004; 58:2133–2143. [PubMed: 15562680]
- Horvitz CC, Ehrlén J, Matlagá D. Context-dependent pollinator limitation in stochastic environments: Can increased seed set overpower the cost of reproduction in an understory herb? *Journal of Ecology*. 2010; 98:268–278.
- Horvitz CC, Schemske DW. Spatiotemporal variation in demographic transitions for a tropical understory herb: projection matrix analysis. *Ecological Monographs*. 1995; 65:155–192.
- Horvitz CC, Tuljapurkar S, Pascarella JB. Plant-animal interactions in random environments: habitat-stage elasticity, seed-predators and hurricanes. *Ecology*. 2005; 86:3312–3322.
- Houle D. Comparing evolvability and variability of quantitative traits. *Genetics*. 1992; 130:195–204. [PubMed: 1732160]
- Hurrell JW. Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science*. 1995; 269:676–679. [PubMed: 17758812]
- Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gilbert P, Beerli P. The strength of phenotypic selection in natural populations. *American Naturalist*. 2001; 157:245–261.
- Lande R. Quantitative genetic analysis of multivariate evolution, applied to brain-body size allometry. *Evolution*. 1979; 33:402–416.
- Lande R. A quantitative genetic theory of life history evolution. *Ecology*. 1982; 63:607–615.
- Lande R, Arnold S. The measurement of selection on correlated characters. *Evolution*. 1983; 37:1210–1226.
- MacArthur R. Selection for life tables in periodic environments. *American Naturalist*. 1968; 102:381–383.
- Pascarella JB, Horvitz CC. Hurricane disturbance and the population dynamics of a tropical understory shrub: megamatrix elasticity analysis. *Ecology*. 1998; 79:547–563.
- Seneta, E. Non-negative matrices and Markov chains. 2. New York: Springer-Verlag; 1981.
- Schemske DW, Horvitz CC. Variation among floral visitors in pollination ability: A precondition for mutualism specialization. *Science*. 1984; 225:519–521. [PubMed: 17750855]
- Schemske DW, Horvitz CC. Temporal variation in selection on a floral character of a neotropical herb. *Evolution*. 1989; 43:461–464.
- Siepielski AM, DiBattista JD, Carlson SM. It's about time: the temporal dynamics of selection in the wild. *Ecology Letters*. 2009; 12:1261–1276. [PubMed: 19740111]
- Tuljapurkar S. Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theoretical Population Biology*. 1982a; 21:114–140.
- Tuljapurkar S. Population dynamics in variable environments. III. Evolutionary dynamics of r-selection. *Theoretical Population Biology*. 1982b; 21:141–165.
- Tuljapurkar S. *Population Dynamics in Variable Environments*. New York: Springer-Verlag; 1990.
- Tuljapurkar S, Horvitz CC. From stage to age in variable environments: life expectancy and survivorship. *Ecology*. 2006; 87:1497–1509. [PubMed: 16869426]
- Tuljapurkar S, Horvitz CC, Pascarella JB. The many growth rates and elasticities of populations in random environments. *American Naturalist*. 2003; 162:489–502.
- van Tienderen PH. Elasticities and the link between demographic and evolutionary dynamics. *Ecology*. 2000; 81:666–679.

Appendix 1

Illustrations of Markov chains for two different models of environmental dynamics for each study species, Calathea (1A, 1B) and Red Deer (1C, 1D). Climate-based models of environmental change are in 1A (rainfall in the dry season) and 1C (NAO index), while alternate models are in 1B (environmental constancy), 1D (the observed temporal pattern over the 26 years of the study is the most likely trajectory). Diagrams are schematic; sizes of dots represent relative values of transition probabilities among environmental states over one time step.

Figure 1.

Temporal variation in relevant stage-specific demographic rates (1A for *Calathea* and 1C–E for Red Deer) and in mean-standardized stage-specific selection gradients (1B for selection on floral tube length of *Calathea* and 1F–H for selection on time of birth [days after January 1] of Red Deer), calculated using individual stage- and environment-specific demographic rates to measure fitness.

Figure 2.

Temporal variation in the overall environmental quality as measured by the population growth rate λ associated with the population projection matrix calculated from the full set of demographic rates for Calathea (2A) and Red Deer (2B) for each temporal state of the environment.

Figure 3.

Study years (in red) in the context of long-term climate data, rainfall in the dry season for Calathea (3A) and the North Atlantic Oscillation (NAO) index for Red Deer (3B); data are expressed as the annual deviation from the mean divided by the standard deviation.

Figure 4.

Normalized environment-specific elasticity (4A, 4C) and normalized environment-specific integrated selection (4C, 4D) for reproduction under two different models of environmental dynamics (4A and 4C show results for the model based on rainfall in the dry season; 4B and 4D show results for the model based on an assumption of environmental constancy) for *Calathea*.

Figure 5.

Normalized environment-specific elasticity for reproduction (5A, 5C) and survival (5B, 5D) under two different models of environmental dynamics (5A and 5B show results for the model based on NAO index; 5C and 5D show results for the model based on an assumption of that the observed temporal pattern over the 26 years of the study is the most likely trajectory) for Red Deer.

Figure 6.

Normalized environment-specific integrated selection for reproduction (6A, 6C) and survival (6B, 6D) under two different models of environmental dynamics (6A and 6B show results for the model based on NAO index; 6C and 6D show results for the model based on an assumption of that the observed temporal pattern over the 26 years of the study is the most likely trajectory) for Red Deer.

Figure 7.

Integrated selection summed across all environments by life-history rate (reproduction and, where relevant, survival, of each stage) under two different models of environmental dynamics for each study species, *Calathea* (7A, 7B) and Red Deer (7C, 7D). Climate-based models of environmental change are in 7A (rainfall in the dry season) and 7C (NAO index), while alternate models are in 7B (environmental constancy), 7D (the observed temporal pattern over the 26 years of the study is the most likely trajectory). Total integrated selection summed across all life-history paths and environments is given at the top of each panel for reference (it is also in Table 2).

Figure 8.

Integrated selection summed across all life history rates by environment under two different models of environmental dynamics for each study species, *Calathea* (8A, 8B) and Red Deer (8C, 8D). Climate-based models of environmental change are in 8A (rainfall in the dry season) and 8C (NAO index), while alternate models are in 8B (environmental constancy), 8D (the observed temporal pattern over the 26 years of the study is the most likely trajectory). Additionally, its summation by NAO category is shown in 8E, obtained from adding individual-year environments according to the category to which they each belong.

Table 1Proportion of Each Environmental State in the Stationary Distribution of Environments, π_{β}

State of the environment	Model of environment change			
	<i>Calathea</i>		Red deer	
	Dry season	Stasis	NAO	26-yr cycle
1	.3377	.1667	.0506	.0385
2	.3234	.2222	.0395	.0385
3	.2681	.2778	.0568	.0385
4	.0707	.3333	.0426	.0385
5			.0452	.0385
6			.0546	.0385
7			.0486	.0385
8			.0112	.0385
9			.0513	.0385
10			.0524	.0385
11			.0551	.0385
12			.0519	.0385
13			.0539	.0385
14			.0071	.0385
15			.0113	.0385
16			.0458	.0385
17			.012	.0385
18			.0336	.0385
19			.0108	.0385
20			.0102	.0385
21			.0426	.0385
22			.0457	.0385
23			.0498	.0385
24			.0497	.0385
25			.0306	.0385
26			.0372	.0385

Note. NAO = North Atlantic Oscillation.

Table 2
Stochastic Growth Rate (λ_s) of the Population and Total Integrated Selection on the Trait

	Model of environmental change			
	<i>Calathea</i>		Red deer	
	Dry season	Stasis	NAO	26-yr cycle
λ_s	.9887	.9867	1.0275	1.017
Total integrated selection	-.1731	-.1083	-.2471	-.2892

Note. NAO = North Atlantic Oscillation.