



Is life-history buffering or lability adaptive in stochastic environments?

David N. Koons, Samuel Pavard, Annette Baudisch and C. Jessica E. Metcalf

D. N. Koons (david.koons@usu.edu), Dept of Wildland Resources and the Ecology Center, Utah State Univ., 5230 Old Main Hill, Logan, UT 84322, USA. – DNK, S. Pavard, A. Baudisch and C. J. E. Metcalf, Max Planck Inst. for Demographic Research, Konrad-Zuse Str. 1, DE-18057 Rostock, Germany. SP also at: Mus. Natl d'Histoire Naturelle, FR-75016 Paris, France. CJEM also at: Duke Population Res. Inst., Duke Univ., Durham, NC 27707, USA.

It is commonly thought that temporal fluctuations in demographic parameters should be selected against because of the deleterious impacts variation can have on fitness. A critical underpinning of this prediction is the assumption that changes in environmental conditions map linearly into changes in demographic parameters over time. We detail why this assumption may often break down and why selection should not always favor buffering of demographic parameters against environmental stochasticity. To the contrary, nonlinear relationships between the environment and demographic performance can produce asymmetric temporal variation in demographic parameters that actually enhances fitness. We extend this result to structured populations using simulation and show that ‘demographic lability’ rather than ‘buffering’ may be adaptive, particularly in organisms with low juvenile or adult survival. Finally, we review previous ecological work, and indicate cases where ‘demographic lability’ may be adaptive, then conclude by identifying research that is needed to develop a theory of life-history evolution that encompasses both demographic buffering and lability.

Temporal variability in the environment can change demographic parameters (i.e. survival, fertility, etc.) and eventually lead to the evolution of life history strategies that differ from those that are optimal in constant environments (Tuljapurkar 1990, Orzack and Tuljapurkar 2001, Metcalf and Koons 2007). A key prediction of the theory about evolution in stochastic (i.e. randomly variable) environments is that variability in short-term fitness around its mean leads to a reduction in long-term fitness (Eq. 2, Lewontin and Cohen 1969, Tuljapurkar 1982, 1990). Based on this premise, Gillespie (1977) suggested that natural selection should favor demographic parameters that are highly buffered against (i.e. robust to) temporal variation in the environment. Using sensitivity and elasticity analyses of empirical data for a large range of taxonomic orders, Pfister (1998) concluded that there was strong empirical evidence that natural selection had favored buffering in demographic parameters with a large impact on Malthusian fitness (see Morris and Doak 2004 for corrections to this analysis).

Now known as the demographic buffering hypothesis (Boyce et al. 2006), the popular view is that buffering is a widespread evolutionary outcome (Pfister 1998), and arises because of selection for alleles yielding demographic parameters that are robust to environmental change. This hypothesis, and in fact, most studies on life history evolution in stochastic environments, are contingent on the assumption that changes in environmental conditions

map linearly into changes in demographic parameters over time (Morris et al. 2008). Although not yet considered within an evolutionary framework, it is known in ecology that the negative effect of environmental variability on population growth is not ubiquitous. Payne and Wilson (1999) proved that common nonlinear relationships between the environment and demographic parameters can lead to positive effects of environmental stochasticity on population growth (so can the Markovian process of temporally autocorrelated environments, Tuljapurkar et al. 2003, Morris et al. 2006, Tuljapurkar and Haridas 2006, and strong negative co-variation between demographic parameters, Doak et al. 2005). An alternative to the demographic buffering hypothesis may thus be needed to gain a deeper understanding of life history evolution in stochastic environments.

Here, we define adaptive ‘demographic lability’ as the result of selection for alleles favoring demographic parameters that fluctuate freely with temporal changes in the environment; the opposite of being buffered. In a broad sense, demographic lability could encompass both passive (i.e. conformable) and active (i.e. phenotypic plasticity) phenotypic responses to environmental change (Kussell and Leibler 2005). The aim of our paper is to 1) bring adaptive demographic lability to the attention of evolutionary ecologists, 2) determine whether it is possible for organisms with (st)age-structured life cycles to evolve demographic lability, and if so, identify those most likely to do so, 3)

review the current evidence for demographic lability in relation to theoretical predictions, and 4) identify areas of research needed to help develop a more holistic understanding of life history evolution that encompasses both demographic buffering and lability.

The adaptive basis for demographic lability

The notion that demographic buffering holds a selective advantage over lability in stochastic environments may stem from cursory interpretation of how fluctuating environmental conditions affect fitness. Simple nonlinear relationships between environmental conditions and demography (i.e. reaction norms) can actually lead to the exact opposite prediction. To help clarify how nonlinear reaction norms alter stochastic evolutionary dynamics, we focus on independent and identically distributed (I.I.D.) environments (which have symmetric temporal distributions). For I.I.D. environments it is well known that temporal variation ($\sigma^2 = \text{Var}[\ln \lambda(t)]$) in the short-term growth of a strategy ($\ln \lambda(t) = \ln[N(t+1)/N(t)]$, where N denotes a strategy's abundance) reduces long-term fitness ($\ln \lambda_s$) relative to that in constant mean demographic conditions ($\ln \bar{\lambda}$):

$$\ln \lambda_s \cong \ln \bar{\lambda} - \frac{\sigma^2}{2} \quad (1)$$

(Tuljapurkar 1982). This small-noise approximation to fitness in a stochastic environment clearly indicates that both the mean ($\ln \bar{\lambda}$) and variance (σ^2) of growth across environmental conditions affect fitness. In practice, the full expansion for fitness in a stochastic environment:

$$\ln \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} \ln(N(t)) \quad (2)$$

is computed as

$$\ln \lambda_s = \frac{1}{T} \sum_{t=0}^{T-1} \ln \lambda(t) \quad (3)$$

where T is a large number denoting time horizon (Eq. 1–3 applicable to both unstructured (Lewontin and Cohen 1969) and structured populations (Heyde and Cohen 1985)).

As previously stated, the demographic buffering hypothesis is based on assumptions of linear reaction norms (Morris et al. 2008). When true, environmental variation will affect the variance of demographic parameters (and thus σ^2), but not the mean values (Fig. 1, solid black lines); thus guaranteeing a reduction in $\ln \lambda_s$ (Eq. 1) and selection against demographic lability in favor of buffering.

Although this simplifying assumption is often used, nonlinear reaction norms are nonetheless common in nature (Ruel and Ayres 1999). For convex reaction norms (second derivative >0), Jensen's inequality (Hölder 1889, Jensen 1906) guarantees that environmental variation will produce non-additive (skewed) variability in a demographic parameter that increases its temporal mean relative to performance in a constant environment (Fig. 1, dashed green lines; see also Real and Ellner 1992, Pásztor et al. 2000), which will subsequently enhance fitness and select for demographic lability if $\ln \bar{\lambda}$ increases by a large

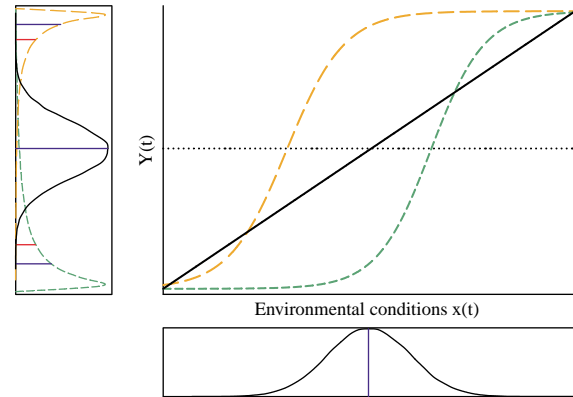


Figure 1. Four hypothetical reaction norms between environmental conditions (x) and any demographic parameter Y . The lower box illustrates mean environmental conditions (blue bar) and its temporal distribution. The left box indicates resulting temporal distributions of $Y(t)$ for each curve (i.e. reaction norm) in the main figure (blue bars indicate $Y(t)$ in average environmental conditions, and red bars indicate the temporal mean of $Y(t)$ across all environmental conditions \bar{Y}). Depending on the reaction norm, environmental stochasticity may decrease (orange dashed lines), have no effect (black solid lines), or increase (green dashed lines) \bar{Y} relative to its value in average environmental conditions. The black dotted line serves a reference where $Y(t)$ is perfectly robust to environmental change.

enough amount to offset the deleterious impacts of σ^2 (Eq. 1). Of course, in the context of pessimistic demographic parameters like the risk of mortality or the probability of death (Preston et al. 2001), increased environmental variation across a convex reaction norm would result in the doubly negative impact of decreased $\ln \bar{\lambda}$ and increased σ^2 ; thereby resulting in selection for buffering. (Note: when environmental stochasticity causes additive (symmetric) temporal variation in the risk of mortality, or its log, the corresponding survival probability will exhibit non-additive variation; Appendix 1). Relative to convex reaction norms, environmental variation across concave reaction norms (second derivative <0) leads to the exact opposite predictions for all demographic parameters (Fig. 1, dashed orange lines). Lastly, if a reaction norm has an inflection point, such that it is convex over part of the range and concave over another part, the effect of environmental stochasticity on a demographic parameter will depend on where the distribution of environmental conditions lay along the reaction norm (Fig. 1).

Thus, nonlinear reaction norms result in selection for lability whenever temporal variation in a demographic parameter increases $\ln \bar{\lambda}$ (via increased mean levels of survival, fertility, etc.) by a large enough amount to offset the deleterious impacts of σ^2 (Eq. 1). In all other cases selection will favor demographic buffering. While studying population persistence and extinction, Payne and Wilson (1999) derived analytical proofs that support this statement. Using a seasonal model for unstructured populations (p. 305), they proved that given a convex relationship between environmental conditions and survival or reproductive output, temporal variation in either parameter can actually increase the long-term abundance of a population (i.e. $N(t)$ as $t \rightarrow \infty$; pp. 308, 313–314); or in an evolutionary context, the long-term abundance and fitness of a ‘strategy’ (see our

Eq. 2). Mathematically, there is thus good reason to believe that demographic lability could evolve as an adaptive strategy in organisms lacking structure in their life cycle.

Most organisms, however, have life cycles with some degree of age or stage structure (Stearns 1992). In the advent of predicted increases in environmental variability induced by climate change (Salinger 2005, IPCC 2007), recent studies indicate that organisms with fast (st)age-structured life histories (early maturation, rapid reproduction, and short lifespan) might be more susceptible to such changes than those with slower, more buffered life histories (Morris et al. 2008, Dagleish et al. unpubl.). We might thus predict that, when reaction norms are linear (an acknowledged assumption in these studies), organisms with buffered (st)age-structured life histories will hold the adaptive advantage and prevail in the future. Below, we explore the implications of nonlinear reaction norms on these evolutionary predictions.

Adaptive demographic lability in structured life history strategies

Life history and environmental models

Fluctuating (st)age-structure in a changing environment presents a difficult challenge for extending Payne and Wilson's proof (1999) to organisms with structured life histories. Nevertheless, we can use numerical simulation to provide initial insight into some of the implications that nonlinear reaction norms have on the evolution of (st)age-structured life histories in stochastic environments.

As an example, consider the following stage-structured life history model with demographic parameters that can vary over time:

$$A(t) = \begin{bmatrix} 0 & F(t) \\ P_J(t) & P_A(t) \end{bmatrix} \quad (4)$$

where $F(t)$, $P_J(t)$ and $P_A(t)$ denote time-specific fertility, juvenile survival, and adult survival respectively (for a model with more structure and age-specificity in the demographic parameters, Appendix 2). By projecting structured abundance n over a long period of time with

$$n(t+1) = A(t)n(t) \quad (5)$$

fitness can be evaluated using Eq. 2 and 3 whereby $N(t) = \Sigma_i n_i(t)$, and $n_i(t)$ denotes the i th component of vector $n(t)$. To make this model amenable to a wide variety of life histories, we defined the time scale as the average time required for juveniles to mature and begin reproduction (i.e. recruit). Let $\hat{\cdot}$ denote a value experienced in average environmental conditions. We then simulated 20 000 life histories by randomly generating values of \hat{P}_J and \hat{P}_A from independent uniform distributions, and solved for values of fertility that yielded replacement-level fitness in a constant average environment ($\hat{F} = (1 - \hat{P}_A)/\hat{P}_J$ yields $\bar{\lambda} = 1$ and $\ln \bar{\lambda} = 0$).

Environmental conditions in time step t were denoted by $x(t)$, where increasing values of $x(t)$ correspond to increasing quality of the environment. To model stochastic environments with different levels of variability, we defined the average environment as $\overline{x(t)} = 0$, and then generated deviates from a normal distribution with mean 0 and

increasing levels of variation to obtain sequences of environmental conditions through time, x , such that $x \sim N(0, \sigma)$ ($\sigma = 0.1, 0.5$ and 0.9 were considered). These sequences of environmental conditions could represent, for example, temperature, precipitation, predator abundance, or a range of other biotic and abiotic variables. To explore the impact of environmental variation across nonlinear reaction norms on each life history's evolutionary fitness, we set the time horizon to $T = 50\,000$ and used a flexible logistic reaction norm to link a demographic parameter, $Y(t)$, to environmental conditions at each time step:

$$Y(t) = \frac{a}{1 + be^{-x(t)}} \quad (6)$$

where the minimum possible value of $Y(t)$ was always 0, a is a constant defining the maximum, and b is a constant defining shape. Because survival probabilities are naturally bounded between 0 and 1, a was set to 1 when either $P_J(t)$ or $P_A(t)$ changed with environmental variation. For each life history, b was always chosen such that $Y(t)$ in the average environment ($\overline{x(t)} = 0$) yielded \hat{Y} as defined above (i.e. \hat{P}_J , \hat{P}_A or \hat{F}). Reaction norms for $Y(t)$ were thus concave when $x(t) > \ln b$, and convex when $x(t) < \ln b$. For simplicity, temporal variation in each demographic parameter was examined separately.

Results and predictions

When examining temporal variation in $F(t)$ (with $P_J(t)$ and $P_A(t)$ held fixed at \hat{P}_J and \hat{P}_A , respectively), we found that, if fertility in the average environment \hat{F} was near its maximum a , reaction norms were automatically concave across most environmental conditions. Consequently, environmental variation had a deleterious impact on fitness; resulting in selection for buffered fertility amongst all of the simulated life histories (Fig. 2, solid black area in left pane). Yet, at higher levels of a and \hat{P}_A , labile fertility was selected for because 1) reaction norms were more likely to be convex in the vicinity of \hat{F} , thereby creating situations where good environmental conditions outweighed the impact of bad conditions, and 2) higher \hat{P}_A yielded greater 'storage' of individuals in the adult stage that could take advantage of good reproductive conditions (Chesson 2000; Fig. 2, white area in middle and right panes; Fig. 3 serves as an exemplar 3-dimensional depiction of the middle pane in Fig. 2). Nevertheless, because it is often difficult to define a priori boundaries on fertility, it may be necessary to estimate fertility maxima for a wide variety of organisms before hypotheses about the life-history advantages of labile versus buffered fertility can be entertained.

Survival probabilities, on the other hand, have innate boundaries $[0, 1]$ that produce interesting evolutionary constraints when reaction norms follow sigmoid patterns. For example, we found that life histories with low \hat{P}_J ($< \sim 0.5$) were more likely to experience fitness benefits (white area in left pane of Fig. 4) when $P_J(t)$ fluctuated with environmental variation across a reaction norm that was inherently convex across a broad array of conditions (with $P_A(t)$ and $F(t)$ held fixed at \hat{P}_A and \hat{F} , respectively). Life histories with high \hat{P}_J , however, were more apt to suffer reduced fitness (black area in left pane of Fig. 4) because of a predominantly concave reaction norm. As we

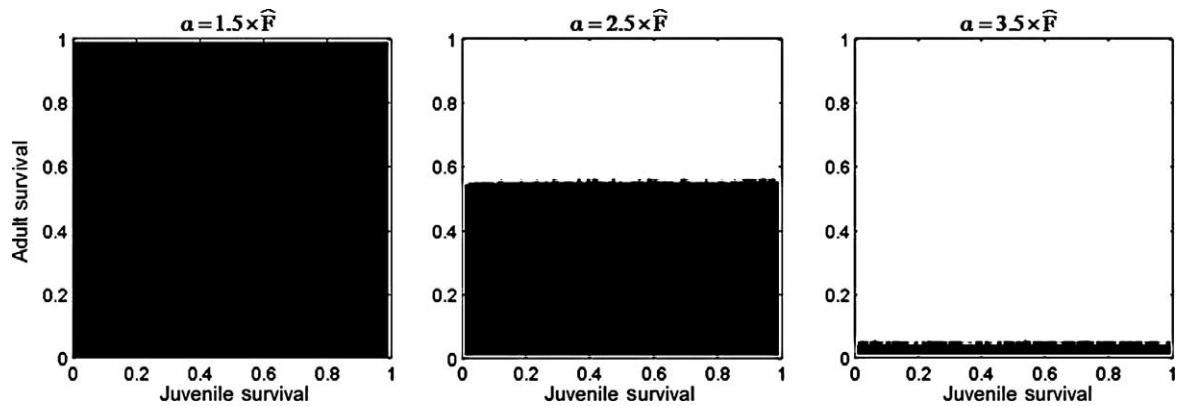


Figure 2. Depictions of whether environmental variation across a nonlinear reaction norm with fertility increased (white; indicating selection for lability) or decreased (black; indicating selection for buffering) fitness of each life history relative to that in a constant environment, according to low, medium, and high maxima α relative to fertility in average environmental conditions ($\sigma = 0.5$ in these examples).

increased environmental variation, levels of \hat{P}_J defining the aforementioned life-history boundary (between those that experience augmented and reduced fitness) generally decreased, but were also tempered by \hat{P}_A (Fig. 4). The same principles applied to temporal fluctuations in $P_A(t)$ across its reaction norm (with $P_J(t)$ and $F(t)$ held fixed at \hat{P}_J and \hat{F} , respectively), and results were quite similar (Fig. 5). Although our focal model has a simple structure, similar conclusions can be drawn from models with more age structure, as well as those with improvement or senescence in survival over the lifespan (Appendix 2).

Natural selection may thus be more apt to favor lability in (st)age-specific survival amongst organisms with low juvenile survival \hat{P}_J or adult survival \hat{P}_A , and buffering in (st)age-specific survival in organisms with high juvenile survival \hat{P}_J or adult survival \hat{P}_A . Therefore, rather than suffering from increased environmental variability induced by climate change (Morris et al. 2008), short-lived organisms might actually benefit from such changes (Drake 2005). On the other hand, organisms with high probabilities of survival could better ensure their fitness prospects by

hedging their bets against environmental uncertainty with buffered demography (Dalglish et al. unpubl.).

We have shown that nonlinear reaction norms have the potential to shed new light on our views about the evolution of (st)age-structured life histories in stochastic environments. Nevertheless, we must remember that the real world is much more complex than our simple simulations depict. Each demographic parameter could have a different reaction norm with each component of the environment (e.g. climate, food, predators, etc.). Furthermore, survival could be affected by a particular environmental variable in a much different way than fertility, and demographic parameters can co-vary together through time (Doak et al. 2005). All of these factors impact fitness ($\ln \lambda_s$) and collectively determine whether lability or buffering is selected for at a given point in the life cycle, which does not preclude the possibility that selection could favor the opposite strategy at another point in the life cycle.

In the absence of proper experiments, demonstrating the adaptive utility of demographic lability will be challenging. Nonetheless, field studies have the power of providing us with important information about life history evolution and population dynamics in our ever-changing world. In the next section, we explore the types of conditions that might favor demographic lability by reviewing the current empirical evidence for its existence in wild populations.

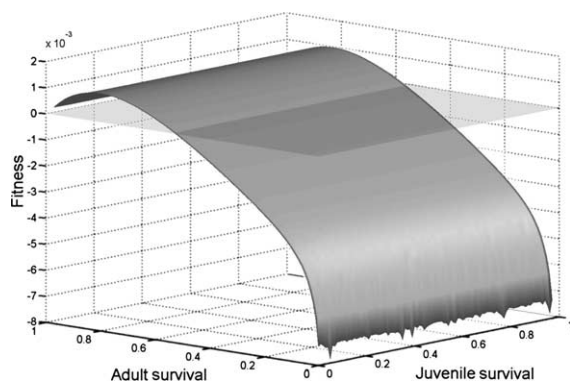


Figure 3. A 3-dimensional depiction of the middle pane in Fig. 2 that shows actual fitness responses (z-axis) of each life history to environmental variation ($\sigma = 0.5$) across a nonlinear reaction norm with fertility ($\alpha = 2.5 \times \hat{F}$). Each life history is distinguished by its values of juvenile survival (x-axis), adult survival (y-axis), and fertility (not shown) in average environmental conditions. The transparent grey plane denotes fitness in constant average environmental conditions (i.e. $\ln \bar{\lambda} = 0$).

Adaptive demographic lability in the wild

Although largely focused on population dynamics, and not evolution per se, the most compelling evidence for demographic lability comes from Drake's (2005) discovery of convex relationships between $\ln \lambda(t)$ and temperature in many species of zooplankton. Although it is not known whether these relationships are driven by fertility, survival, or both, increased temporal variation in temperature induced by climate change has led to widespread increases in zooplankton population growth ($\ln \lambda_s$; Drake 2005). Thus, natural selection in these short-lived organisms may be favoring lability in at least one demographic parameter.

Despite its greater longevity, *Mya arenaria* (a clam) display high levels of temporal variation in recruitment (i.e.

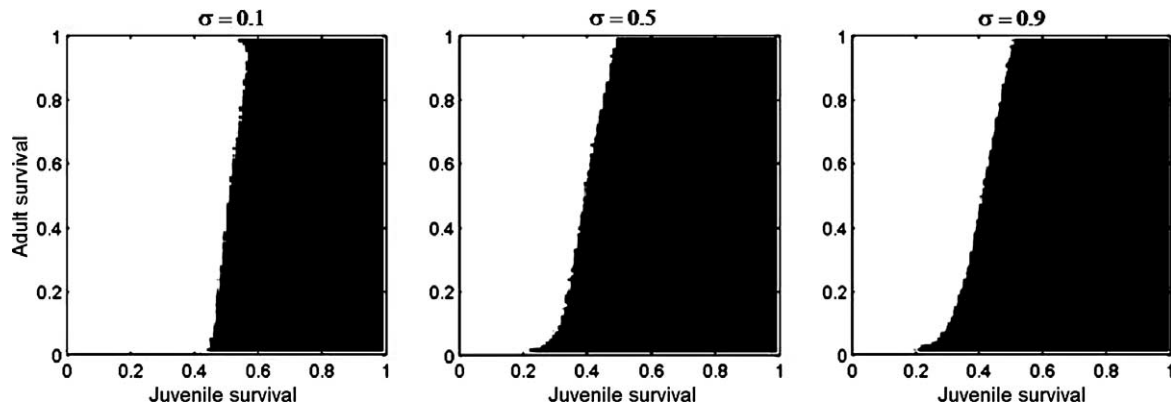


Figure 4. Depictions of whether environmental variation across a nonlinear reaction norm with juvenile survival increased (white; indicating selection for lability) or decreased (black; indicating selection for buffering) fitness of each life history relative to that in a constant environment, according to low, medium, and high levels of environmental variability σ .

lability) that, until recently, could not be explained with adaptive reasoning. In extremely good conditions this species can achieve high rates of recruitment (i.e. large a), but in the average environment, recruitment is well below its potential. As a result, *Mya arenaria* recruitment has a predominantly convex reaction norm with the environment that produces a skewed log-normal distribution over time (similar to dashed green lines in Fig. 1) and positive effects of lability on $\ln \lambda_s$ (Ripley and Caswell 2006). Furthermore, changes in stage-specific *Mya arenaria* recruitment have a larger effect on population growth (elasticity = 0.99) than changes in adult survival (elasticity = 0.01; Ripley and Caswell 2006); indicating that *Mya arenaria* has a life history that does not fit the demographic buffering expectation, whereby parameters having a large impact on population growth should exhibit greater buffering (i.e. low temporal variation; Pfister 1998).

Often kept at low to moderate levels by high rates of predation, nest survival of North American ducks (Hoekman et al. 2002) and adult survival of some African ungulates (Owen-Smith and Mason 2005) also have a large impact on population growth, but their high variability over time provides further evidence against the aforementioned demographic-buffering prediction (but see Gaillard and Yoccoz 2003 for supportive findings). Trophic interactions

may thus be important to consider in the study of demographic lability.

For example, in the presence of heterospecific competitors or predators, environmental stochasticity has been shown to enhance rates of population growth from low density in prairie grasses (Adler et al. 2006) and rabbits *Oryctolagus cuniculus* (Davis et al. 2002). By altering an organism's norms of reaction with its surrounding biotic and abiotic environment, heterospecific organisms might play a fundamental role in driving these beneficial impacts of demographic lability on population growth or fitness (Chesson 2000, Davis et al. 2002).

The evidence for adaptive demographic lability is only beginning to take shape, but is surprisingly consistent with our basic predictions laid out in the previous section. Nevertheless, many more studies with an evolutionary focus will be needed in order to identify the life-history circumstances in which demographic lability operates as an evolutionary adaptation relative to those where buffering holds the advantage.

Concluding remarks

Few organisms are capable of having reaction norms that rapidly approach their maximums (e.g. Fig. 1, orange

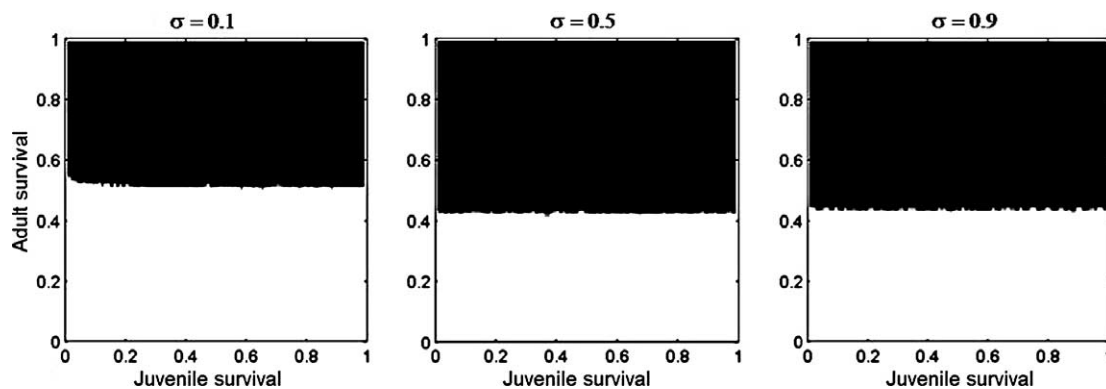


Figure 5. Depictions of whether environmental variation across a nonlinear reaction norm with adult survival increased (white; indicating selection for lability) or decreased (black; indicating selection for buffering) fitness of each life history relative to that in a constant environment, according to low, medium, and high levels of environmental variability σ .

dashed line, and region above it) because of phylogenetic and developmental constraints, interspecific conflicts, and limited resource supplies that drive life-history tradeoffs (Roff 2002). These constraints, and others, have led to the evolution of a wide variety of life history strategies (Stearns 1992), and presumably, a wide variety of demographic reaction norms (e.g. Fig. 1). Our simulations indicate that short-lived organisms with high potential for reproduction (e.g. invasive species) may be more likely to have convex demographic reaction norms that could allow them to benefit from increased environmental stochasticity brought about by climate change (Salinger 2005). If so, this could create a number of new pest- and invasive-species problems for natural resource managers (Drake 2005). Although long-lived species with low capacity for reproduction may be more apt to have concave reaction norms, their highly buffered life histories could help them endure periods of increased environmental stochasticity (Morris et al. 2008, Dalglish et al. unpubl.). Organisms with intermediate life-history strategies, however, may not be able to capitalize on, nor endure, increased environmental stochasticity, and could suffer the most from this aspect of climate change.

Yet, before making definitive predictions about how species will respond to increased environmental stochasticity, we must identify the proximate mechanisms (development, physiology, behavior, etc.) that shape demographic reaction norms, and how these mechanisms respond to change in particular aspects of the environment (i.e. temperature, predators, etc.) (Nussey et al. 2007). Plasticity in traits that affect demographic parameters, however, is not necessarily translated into labile demography; nor is the lack of plasticity necessarily translated into buffered demography. For example, behavioral plasticity enables ectotherms to locate habitats that help moderate body temperature and buffer mortality against external fluctuations in temperature (Martin and Huey 2008). On the other hand, foraging behavior that 'passively' tracks resource availability could lead to large temporal variation in the energy available for reproductive investment, and hence labile reproductive output (McNamara et al. 1991, Kussell and Leibler 2005).

Functions describing the effect of environmental variability on proximate traits (e.g. physiology and behavior), and ultimately demography and fitness, will thus have to be studied in greater detail. Along with experiments and long-term studies, structural equation models could be used to estimate the multifaceted relationships between environment, physiology and behavior, and demography, but comparisons of different linear and nonlinear functions (e.g. using information criteria) should be performed in order to properly identify the functional forms (i.e. shapes) of important reaction norms. Analyses such as these performed across taxa could eventually provide a basis for making general predictions about the evolution of demographic buffering and lability across life histories based on simple trait characters (e.g. endotherm vs ectotherm).

To help guide empirical research, theoretical studies will also be needed to identify the environmental, genetic, reaction-norm, and life history settings where demographic lability can evolve relative to those where it cannot. The implications of nonlinear relationships between demographic parameters and fitness deserve further study within these contexts (Cohen 1980, Caswell 1996). In addition to

more detailed investigations into the implications of nonlinear reaction norms on life history evolution in stochastic I.I.D. environments (our focus), future theoretical studies should also consider the broader implications of more complex, but potentially more realistic, types of stochastic environments; such as those with seasonality and temporal autocorrelation (Tuljapurkar et al. 2003, Drake et al. 2006, Morris et al. 2006, Tuljapurkar and Haridas 2006, Wilmsers et al. 2007). In particular, global climate change is expected to cause simultaneous changes in both the mean and variance of environmental conditions (Salinger 2005). Climate change could thus generate 'time-variant' environmental stochasticity (i.e. a non-stationary distribution of environmental conditions; Caswell 2001), which has not received nearly as much attention as time-invariance (but see Lee and Tuljapurkar 1994 for theory, Gotelli and Ellison 2006 for application in ecology). Consequently, we think that studies on the implications of nonlinear reaction norms in time-variant stochastic environments will be a ripe area for future research. The rates of change in both the mean and variance of environmental conditions relative to generation time could influence whether or not species with favorable reaction norms will be able to adapt to global climate change, and deserves immediate attention.

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Appendix 1

The effects of temporal variation in the risk of mortality on survival probability

With a continuous hazard function describing changes in the instantaneous rates of death over the course of life, h_t , the risk of mortality over a time interval H_t is computed as $H_t = \int_t^{t+\omega} h_u du$ (see Cox and Oakes 1984 for the discrete approximation of H_t). The functional relationship between H_t and the probability of survival over the same time interval (P_t) is given by the nonlinear transformation $H_t = -\ln[P_t]$, and conversely $P_t = \exp[-H_t]$. Thus, P_t is a decreasing convex function of H_t (Fig. A1). Consequently, if environmental stochasticity causes additive temporal variation in H_t , the resulting variation in P_t is multiplicative and skewed in such a way that the mean across all environmental conditions \bar{P}_t is greater than in the average environment \hat{P}_t (Fig. A1, see also Eq. A6 in Payne and Wilson 1999).

Additive-hazard statistical models are commonly used; however, it might be unreasonable to think that environmental stochasticity could cause additive temporal variation in H_t when \hat{H}_t is small because it could lead to negative hazards and undefined survival probabilities. Multiplicative variation in H_t , however, ensures positive hazards and defined survival probabilities (akin to the commonly used proportional hazard, and accelerated failure time models). Multiplicative temporal variation in H_t happens to be equivalent to additive variation in $\ln[H_t]$. Interestingly, the relationship between $\ln[H_t]$ and P_t has an inflection point at $\ln[H_t] = 0$ (which is equivalent to $P_t = 0.37$). To the left of the inflection point the relationship is concave, and to the right it is convex. Consequently, when the log-risk-of-mortality in the average environment ($\ln[H_t]$) is less than zero ($\hat{P}_t > 0.37$), additive temporal variation around

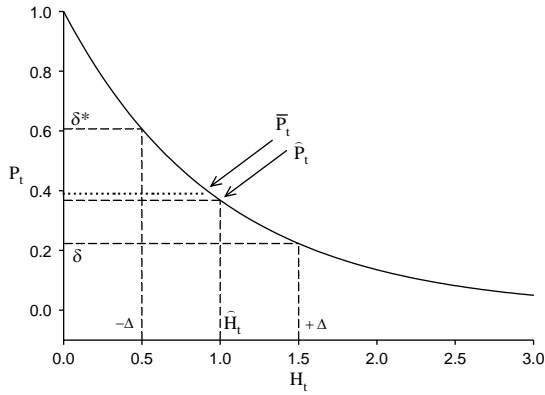


Figure A1. Symmetric deviates ($\pm \Delta$ and dashed drop lines) around the risk of mortality in the average environment \widehat{H}_t lead to asymmetric deviates ($\delta^* > \delta$) around \widehat{P}_t and a higher mean probability of survival across all environmental conditions \overline{P}_t .

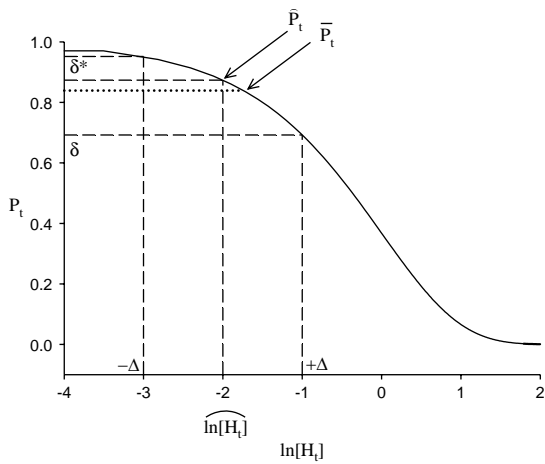


Figure A2. Symmetric deviates ($\pm \Delta$ and dashed drop lines) around a low logged risk of mortality in the average environment $\widehat{\ln[H_t]}$ lead to asymmetric deviates ($\delta^* < \delta$) around \widehat{P}_t and a lower \overline{P}_t .

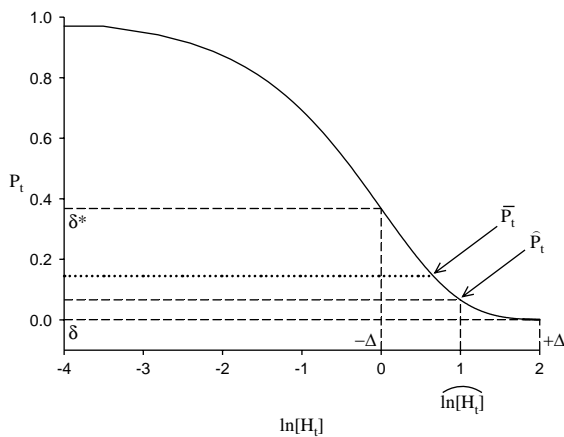


Figure A3. Symmetric deviates ($\pm \Delta$ and dashed drop lines) around a high logged risk of mortality in the average environment $\widehat{\ln[H_t]}$ lead to asymmetric deviates ($\delta^* > \delta$) around \widehat{P}_t and a higher \overline{P}_t .

$\widehat{\ln[H_t]}$ can lead to skewed variation around \widehat{P}_t that results in a lower mean survival across all environmental conditions \overline{P}_t (Fig. A2). Conversely, when $\widehat{\ln[H_t]} > 0$ ($\widehat{P}_t < 0.37$),

additive temporal variation around $\widehat{\ln[H_t]}$ can lead to skewed variation around \widehat{P}_t that results in a higher mean survival across all environmental conditions \overline{P}_t (Fig. A3). Thus, for organisms that experience a low probability of survival in an average environment, environmental stochasticity that drives multiplicative temporal variation in H_t (additive variation in $\ln[H_t]$) can actually improve the mean probability of survival across all environmental conditions.

Appendix 2

Adaptive demographic lability in life histories with age-specific improvements or senescence in survival

Here, we expand upon the results arising from Eq. 4 in the text by considering a matrix model with more structure (10×10), and greater age-specificity in survival:

$$A(t) = \begin{bmatrix} 0 & 0 & \widehat{F} & \cdots & \widehat{F} & \widehat{F} \\ P_J(t) & 0 & 0 & \cdots & 0 & 0 \\ 0 & P_J(t) & 0 & \cdots & 0 & 0 \\ 0 & 0 & P_\alpha(t) & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & P_{\alpha+6}(t) & 0 \end{bmatrix} \quad (B1)$$

where $P_i(t)$ denotes time-specific survival for age class i . For simplicity, fertility (\widehat{F}) was assumed to be constant and independent of age. Fitness in a stochastic I.I.D. environment was evaluated according to Eq. 2, 3 and 5 in the main text. We parameterized age-specific survival in constant average environmental conditions (\widehat{P}_i) with age-independent (β_0) and age-dependent (β_{age}) parameters using a simple logit-linear function:

$$\widehat{P}_i = \frac{e^{\beta_0 + \beta_{age} \times i}}{1 + e^{\beta_0 + \beta_{age} \times i}} \quad (B2)$$

Three sets of 1,000 life histories were created by first generating a sequence of 1,000 β_0 values between -5 and 5 , then setting β_{age} such that survival would senesce (-0.5), stay the same (0), or increase (0.5) across adult age classes (Fig. B1). Moreover, we restricted survival to be

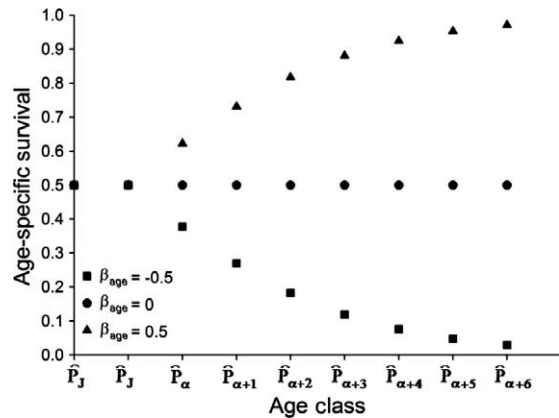


Figure B1. Age-specific survival in constant average environmental conditions according to different values of β_{age} ($\beta_0 = 0$ in this example).

similar across the juvenile age classes, and only allowed changes in age-specific survival to begin once the age at first reproduction (α) had been reached (i.e. $i=1$ for age class α). For each life history, we then solved for values of fertility that yielded replacement-level fitness in a constant average environment ($\bar{\lambda} = 1$ and $\ln \bar{\lambda} = 0$).

Environmental variability was created according to the method described in the main text. We then examined the fitness consequences of environmental variation across a nonlinear reaction norm with the age-independent survival parameter ($\beta_0(t)$) for each life history:

$$\beta_0(t) = \min + \frac{\max - \min}{1 + b e^{-x(t)}} \quad (\text{B3})$$

where b is a constant defining shape and the minimum and maximum values were -10 and 10 , respectively. This created simultaneous temporal variation in all of the age-specific survival probabilities. For each life history, b was always chosen such that $\beta_0(t)$ in the average environment ($\overline{x(t)} = 0$) yielded $\bar{\beta}_0$.

Similar to our findings for the simple 2-stage matrix model (Eq. 4), life histories with low age-independent components of survival were more likely to experience fitness benefits when $\beta_0(t)$ fluctuated with environmental variation across its nonlinear reaction norm (Fig. B2). High environmental variability ($\sigma = 0.5$ and 0.9) greatly improved fitness for life histories with very low survival, but fewer life histories benefited from environmental variability because extreme conditions in the concave portion of the reaction norms were sampled more often; an inherent property of our sigmoid reaction norms. Surprisingly, the different trajectories of age-specific survival over the lifespan (Fig. B1) had very little effect on the fitness results. Life histories with senescence (Fig. B2 1st column), however, experienced a slight advantage over the others (Fig. B2 column 2 and 3) because their survival probabilities tended towards lower values across multiple age classes; a property that seems to be an advantage in a stochastic environment that deserves further study.

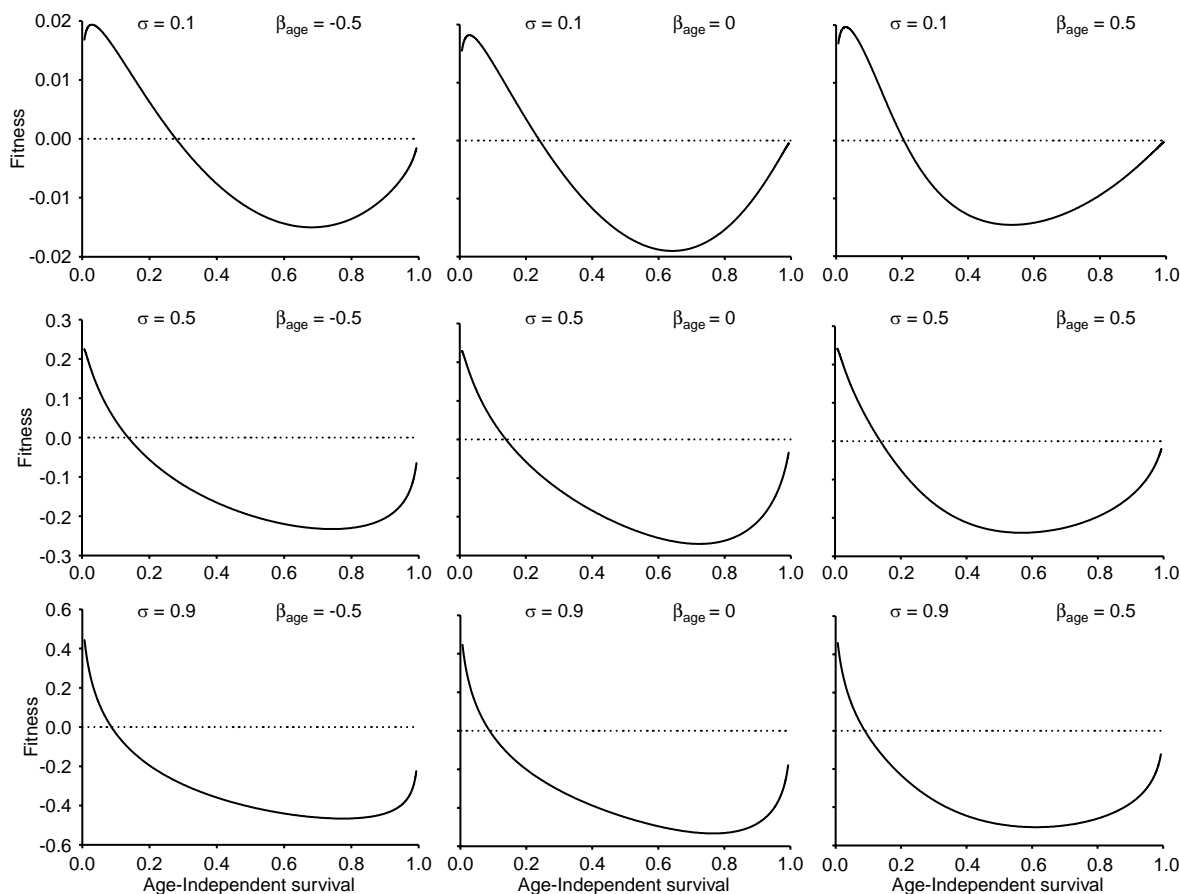


Figure B2. Fitness responses of 1000 life histories to environmental variation ($\sigma = 0.1, 0.5$ or 0.9) across a nonlinear reaction norm with the age-independent survival parameter ($\beta_0(t)$). Each life history is distinguished by its age-independent component of survival in a constant environment (equivalent to \bar{P}_j), and how it increases ($+\beta_{\text{age}}$) or senesces ($-\beta_{\text{age}}$) after the age at first reproduction. The horizontal dotted line denotes fitness in a constant average environment (i.e. $\ln \bar{\lambda} = 0$).