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DOI

[10.1086/675817](https://doi.org/10.1086/675817)

Publication date

2014

Document Version

Final published version

Published in

American Naturalist

[Link to publication](#)

Citation for published version (APA):

Smallegange, I. M., Deere, J. A., & Coulson, T. (2014). Correlative Changes in Life-History Variables in Response to Environmental Change in a Model Organism. *American Naturalist*, 183(6), 784-797. <https://doi.org/10.1086/675817>

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Correlative Changes in Life-History Variables in Response to Environmental Change in a Model Organism

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Submitted June 5, 2013; Accepted December 27, 2013; Electronically published April 21, 2014

Online enhancement: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.df98r>.

ABSTRACT: Global change alters the environment, including increases in the frequency of (un)favorable events and shifts in environmental noise color. However, how these changes impact the dynamics of populations, and whether these can be predicted accurately has been largely unexamined. Here we combine recently developed population modeling approaches and theory in stochastic demography to explore how life history, morphology, and average fitness respond to changes in the frequency of favorable environmental conditions and in the color of environmental noise in a model organism (an acarid mite). We predict that different life-history variables respond correlatively to changes in the environment, and we identify different life-history variables, including lifetime reproductive success, as indicators of average fitness and life-history speed across stochastic environments. Depending on the shape of adult survival rate, generation time can be used as an indicator of the response of populations to stochastic change, as in the deterministic case. This work is a useful step toward understanding population dynamics in stochastic environments, including how stochastic change may shape the evolution of life histories.

Keywords: bulb mite *Rhizoglyphus robini*, integral projection models, perturbation analysis, slow-fast life-history continuum, stochastic population growth rate.

Introduction

Environmental change greatly influences the dynamics of populations (Andrewartha and Birch 1954; Boyce et al. 2006) and can generate simultaneous responses in population fluctuations, life history, and phenotype distributions (Hairston et al. 2005; Coulson et al. 2011). However, the wide range of observed and expected ecological and evolutionary responses to changes in environmental conditions (Reznick et al. 2001; Post et al. 2009; Coulson et al. 2011) means that understanding the population consequences of environmental change has become one of the

greatest challenges in biology (Schoener 2011). This challenge is even more current today as several aspects of the environment are changing simultaneously: the frequency of ecological and climate events (e.g., algal blooms or El Niño years) is increasing and there have also been temporal changes in the amplitude and probability distribution of climate variables (Emanuel 2005; Katz et al. 2005; García-Carreras and Reuman 2011). Detailed investigations into the consequences of such changes largely fall into two groups. The first group uses data from field populations to decompose variation in demographic rates into different ecological and/or evolutionary contributions (Coulson et al. 2001; van de Pol et al. 2010), and it also uses data from field populations to assess how populations respond to perturbation of demographic rates (e.g., Forcada et al. 2008; Morris et al. 2008; Dalglish et al. 2010; Coulson et al. 2011) and to recurrent disturbances (e.g., Tuljapurkar et al. 2003; Barrows et al. 2010; Vincenzi et al. 2012). The second group consists of theoretical studies that investigate the demography of populations and stylized life histories in stochastic environments (e.g., Wilmsers et al. 2007; Lande et al. 2009; Tuljapurkar et al. 2009). Results from the first group of studies indicate that the relative importance of specific demographic rates to the growth rate of populations can depend on the frequency of disturbances (Tuljapurkar et al. 2003). They also forecast that the population growth rate of longer-lived species will be less sensitive to increases in climate variability (Morris et al. 2008; Dalglish et al. 2010) but that the population consequences of a change in climate variability can be outweighed by the consequences of changes in the mean environment (van de Pol et al. 2010; Coulson et al. 2011). The theoretical studies, in turn, indicate that a change in the serial correlation of demographic rates may increase or decrease population growth rate depending on the structure of the life history (Tuljapurkar et al. 2009) and that a change in the magnitude or type of environmental stochasticity can induce a shift from fast to slow life histories (Lande et al.

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Am. Nat. 2014. Vol. 183, pp. 784–797. © 2014 by The University of Chicago. 0003-0147/2014/18306-5471\$15.00. All rights reserved.
DOI: 10.1086/675817

2009) or even lead to extinction due to increased population fluctuations (Wilmers et al. 2007). These are notable insights but the question of how common concurrent change in life-history variables such as the population growth rate, generation time, and lifetime reproductive success is in response to changing environmental change, is still open. In a recent study, Coulson et al. (2011) concluded from their analysis on the demography of Yellowstone gray wolves that different types of environmental change can generate a wide range of responses in population biology quantities such as life-history variables. However, only a consistent population response, that is, one where life-history variables show a correlative response to environmental change so that testable predictions on the consequences of environmental change can be derived, improves our understanding of population dynamics in variable environments. Accurate predictions of the life-history response can be achieved when the relationship between a species' life history and its environment is known in great detail (Coulson et al. 2011). We therefore set out to explore the impact of environmental change on the life-history response of a model organism, the bulb mite (*Rhizoglyphus robini*), of which we have detailed knowledge of how environmental quality affects its life history (Smallegange 2011a, 2011b; Smallegange and Coulson 2011). To this end, we combine recently developed population modeling approaches and theory in stochastic demography to predict how different life-history variables vary in response to environmental change across a range of stochastic environments.

Changes in environmental conditions translate into changes in demographic rates (Boyce et al. 2006), which can in turn affect the dynamics of a population (Coulson et al. 2011). Integral projection models (IPMs; Easterling et al. 2000) provide a powerful approach to investigate concurrent change in life-history variables within populations (Coulson et al. 2011). Here we develop IPMs for the bulb mite to examine the likely life-history response of populations to changes in important properties of the environment: (i) the temporal frequency of favorable environment states and (ii) the serial correlation of environment states. Investigating population responses to these two types of changes is paramount to understanding the effects of climate change on the dynamics of structured populations (Boyce et al. 2006; Wilmers et al. 2007) and also informs on how stochastic change shapes the evolution of life histories (Tuljapurkar et al. 2009). We use a scenario in which the environment is in one of two states, good or bad, and investigate the life-history response to changes in the environment in four steps. First, we construct the character-demography functions that comprise the good- and bad-environment IPMs and that describe the associations between body size and survival, growth,

and fertility for a population in the good and in the bad environment. Life-history data on bulb mites that were reared on yeast (good environment) and on filter paper (bad environment) are used to parameterize the functions. Yeast is rich in protein, whereas filter paper contains only cellulose on which the mites feed. These two diets represent extremes in terms of food quality and for this reason are commonly used in life-history studies to assess effects of food quality on growth and development of acarid mites (Gerson et al. 1983; Smallegange 2011a, 2011b). This first step will show how character-demography associations and IPM outputs vary between different environment states, which will aid in identifying the drivers that influence these associations. Second, using a stochastic demographic model in which the temporal sequence of good and bad environments is driven by a Markovian process that governs the serial correlation of environment states, a perturbation analysis is conducted to investigate how the two types of environmental change affect the relative importance of demographic rates to the long-run stochastic population growth rate, λ_s . This will reveal if different stochastic environments select for fast life histories, which are characterized by early maturation, short life span, and high fecundity, or for slow life histories that have the opposite characteristics (Stearns 1983; Gaillard et al. 1989; Heppell et al. 2000; for examples of life-history speed in stochastic environments, see Lande et al. 2009; Miller et al. 2011). Note that the latter covariation between age at maturity, fecundity, and survival is captured in the life-history variable generation time (Stearns 1992). Because generation time is directly involved in the calculation of elasticities of λ to vital rates (Hamilton 1966), life-history speed can be linked to demographic sensitivity: the shorter the generation time and the faster the speed of life history, the more sensitive populations are to perturbation of fertility rate, whereas a long generation time is indicative of slower populations that are more sensitive to perturbation of survival rate (Lebreton and Clobert 1991). To cover a wide range of stochastic environments in this second step, the serial correlation varies from blue to red noise color (corresponding to negative and positive first-order autocorrelation of the temporal sequence, respectively), and the frequency at which the good environment occurs varies from zero to one. Third, we examine the response of the stochastic population growth rate (λ_s), generation time, lifetime reproductive success, and body size to assess whether changes in these quantities correlate with changes in the environment so that testable predictions on population responses can be derived. Fourth, and finally, we explore which quantities can be used as indicators of the effects of future environmental change on the growth rate (fitness) of populations and their life-history speed.

Methods

Size- and Stage-Structured Integral Projection Model

The life cycle of the bulb mite comprises five stages: egg ($s = 1$), larva ($s = 2$), protonymph ($s = 3$), tritonymph ($s = 4$), and the adult stage ($s = 5$). We construct a size- and stage-structured integral projection model that tracks the body size distribution of females within each of these stages. Juvenile bulb mites also have a facultative dispersal stage (deutonymph), but few individuals develop into this stage when raised on ad lib. yeast or ad lib. filter paper (Smallegange and Coulson 2011). For simplicity the facultative dispersal stage is not included in the model. The IPM will be parameterized for mites living in a good and in a bad environment (see below).

The rationale of the IPM is as follows. If a female survives from day t to $t + 1$, she stays in the same life stage or moves to the next life stage and then grows from size z to size z' . If a female is an adult, she also produces eggs. In the IPM, these events are captured by statistical, character-demography functions that relate body size z at each time t to: (1) the survival probability at time $t + 1$, $S(s, t, z)$; (2) the transition probability that females stay in stage s at time $t + 1$, $P(s|s, t, z)$; (3a) the increase in body size among survivors that stay in stage s at time $t + 1$, $G(z|s, t, z)$; (3b) the increase in body size among survivors that have moved to stage $s + 1$ at time $t + 1$, $G(z|s + 1, t, z)$; (4) the number of eggs produced at time $t + 1$ (assuming a prebreeding census), $R(s, t, z)$; and (5) the size of eggs produced at time $t + 1$, $D(z|s, t, z)$. Functions (3) and (5) are probability density functions that not only describe how body size at time $t + 1$ is related to body size at time t among survivors but also describe how the variance in size at time $t + 1$ is affected by size at time t among survivors. These functions therefore capture how individuals of identical size at time t can develop to different sizes and produce eggs of different sizes at time $t + 1$. Denoting the number of females of stage s at time t by $n(s, t, z)$ means that the dynamics of this number distribution from t to $t + 1$ can be written as

$$\begin{aligned} n(1, t + 1, z) = & \int_{\Omega_s} D(z|s, t, z') \\ & \times R(s, t, z') n(s, t, z') dz', \end{aligned} \quad (1a)$$

where $s = 5$,

$$\begin{aligned} n(s + 1, t + 1, z) = & \int_{\Omega_s} G(z|s + 1, t, z') \\ & \times P(s + 1|s, t, z') S(s, t, z') \\ & \times n(s, t, z') dz', \end{aligned} \quad (1b)$$

$$\begin{aligned} n(s, t + 1, z) = & \int_{\Omega_s} G(z|s, t, z') P(s|s, t, z') \\ & \times S(s, t, z') n(s, t, z') dz', \end{aligned}$$

where $1 \leq s \leq 4$, and

$$\begin{aligned} n(5, t + 1, z) = & \int_{\Omega_s} G(z|s, t, z') P(s|s - 1, t, z') \\ & \times S(s - 1, t, z') n(s - 1, t, z') dz' \\ & + \int_{\Omega_s} G(z|s, t, z') S(s, t, z') \\ & \times n(s, t, z') dz', \end{aligned} \quad (1c)$$

where $s = 5$. The closed interval Ω_s denotes the size domain of stage s . Since only adults reproduce, the $R(s, t, z)$ and $D(z|s, t, z')$ functions are zero for $1 \leq s \leq 4$ (eq. [1b]). The number distribution of adult females at time $t + 1$ (eq. [1c]) is determined by the number of tritonymphs that have moved to the adult stage at time t (first part of eq. [1c]) and by the number of surviving adult females at time $t + 1$ (second part of eq. [1c]).

Equations (1) describe the dynamics of the continuous trait body size z . Predicted values from these equations are calculated by dividing the size domain of each stage (Ω_s) into very small-width discrete bins, defined as “mesh points,” to create a discrete approximation of the IPM. For each stage, each transition rate was estimated for the midpoint of two adjacent mesh points. The numerical accuracy of the approximation increases with the number of mesh points (Ellner and Rees 2006), and here, the body size domain of each stage was divided into 50 size bins (because body size domains differed between life stages, bin widths differed between life stages; fig. 1). A higher number of bins did not produce different results. The asymptotic population growth rate λ_0 was estimated as the dominant eigenvalue of the resulting 250×250 matrix (there are 50 size bins $\times$ 5 stages = 250 mesh points). We furthermore calculated the key life-history variables generation time (T) and lifetime reproductive success (R_0). Lifetime reproductive success was calculated as the dominant eigenvalue of the matrix $\mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}$, where $\mathbf{I}$ is the identity matrix and $\mathbf{F} = \mathbf{D}\mathbf{R}$, where $\mathbf{D}$ is a matrix that

Figure 1: Character-demography functions for each of the five life stages showing the relationships between body length and survival, fertility, transition rate of moving to the next life stage, and mean growth rate when staying in the same life stage, which are used to parameterize the good-environment integral projection model (IPM; dashed lines and squares) and the bad-environment IPM (solid lines and triangles). Statistical functions that are not displayed are those that describe inheritance; in this specific case, egg size was independent of maternal size so that the expected mean egg size and variance at time $t + 1$ are constant (see also appendix) and growth when growing into the next life stage (in which case growth between time t and $t + 1$ is described by the growth rate of stage $s + 1$, as shown in this figure). Lines represent predictions from regressions, and points represent raw data. In the bottom panels the zero-growth line is also plotted. Growth of the largest adults in the bad environment was not measured, which is why the fitted line—which ranges from the minimum to the maximum observed adult body length—in the bottom right corner panel extends beyond the data points. The size of the smallest and largest individual observed within each life stage determined the minimum and maximum size of the size domain of each life stage.

approximates the inheritance kernel and $\mathbf{R}$ is a matrix that approximates the reproduction kernel. The matrix $\mathbf{T}$ is given by $\mathbf{T} = \mathbf{GS}$, where $\mathbf{G}$ is a matrix that approximates the growth kernel and $\mathbf{S}$ is a matrix that approximates the survival kernel (Caswell 2001, 2009). Generation time was approximated as $T = \log(R_0)/\log(\lambda)$ (Coale 1972; Caswell 2001).

Data Collection

We parameterized the good and bad environment IPMs using life-history data on mites that were reared individually on ad lib. access to yeast (good environment) and ad lib. access to filter paper (bad environment), respectively. Data on the growth and survival of adult females,

egg production, and the relationship between size of the mother and her offspring were taken from Smallegange (2011a, 2011b). Data on juvenile growth and survival were collected here following the methods of Smallegange (2011a, 2011b) and which is described in the appendix, available online. All data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.df98r> (Smallegange et al. 2014).

Parameterizing the Character-Demography Functions

For each IPM, parameters of five character-demography functions were estimated: (1) the survival function; (2) the transition function, which gives the probability of moving from the current life stage to the next; (3) the

growth function; (4) the reproduction function, which gives the number of female offspring produced; and (5) the inheritance function, which gives the relationship between size of the mother and size of her eggs. To construct functions (1)–(5), generalized linear mixed models (GLMMs) were used with body length and body length squared as linear predictors and, except for function (5) where a GLM was used, mite identity as a random factor. The response variables respectively were (1) survival at time $t + 1$ (0 or 1), (2) probability of growing to the next stage at time $t + 1$, $\gamma_{s,t+1}$, (3) mean and variance in body size at time $t + 1$, (4) the number of eggs produced at time $t + 1$, and (5) mean and variance in size of eggs produced at time $t + 1$ by each individual at time t . Eggs do not increase in size so that their size at time $t + 1$ equaled their size at time t .

During data collection it was not always possible to locate each individual every day. For those individuals that were not seen but were alive (e.g., that were seen alive the next day), omitting these observations would result in an underestimation of the survival function. Therefore, we filled in these missing values by estimating the body length of a female of age a using the Gompertz function (fig. A1; figs. A1–A8 available online):

$$z_a = z_\infty e^{-e^{-k(a-a_0)}}, \quad (2)$$

where z_a is body length (μm) at age a (days), z_∞ is the mean maximum length (μm , at $a = \infty$), k is the instantaneous growth rate at age a_0 , and a_0 is the inflection point of the curve and the age at which absolute growth rate begins to decline. Mean maximum length of females was calculated using data from Smallegange (2011a, 2011b). We did not use alternative growth models such as the logistic or von Bertalanffy growth model. The reasons for this is that the von Bertalanffy growth model is not applicable to sigmoidal growth data (unless the cubic version is used, which requires estimating an additional parameter). In the logistic model, in turn, the regions above and below the inflection point are symmetrical, whereas those of the Gompertz function are not. Since our data are not symmetrical around the inflection point, we chose the Gompertz function. It turned out that on the filter paper diet, the survival probability of juveniles of all stages was unaffected by body length (or body length squared) and did not differ between juvenile life stages. Therefore, we lumped survival data of all juveniles and estimated daily survival probability from a survivorship function by estimating the slope of the regression of log-transformed proportion of surviving mites against age (Caswell 2001; fig. A2). For function (2), we used the notion that the probability of growing to the next stage depends on the time spent in the current stage (Caswell 2001) so that $\gamma_{s,t+1}$ is given by $\gamma_{s,t+1} = 1/d_{s,t}$ where $d_{s,t}$ is the number

of days left in stage s , or in other words, the number of days left prior to molting into the next stage $s + 1$. This means that d_s equals the total duration of stage s on the first day that a female is in stage s , and that when an individual develops from stage s into stage $s + 1$ at time $t + 1$, $d_s = 1$ so that $\gamma_{s,t+1} = 1$.

For functions (1), (2), and (4), a model simplification procedure was used whereby the full model was fitted, after which the least statistically significant term was removed (starting with body length squared) if the deletion caused an insignificant increase in deviance (significance was assessed by performing a likelihood ratio test). This procedure was repeated until the model only contained significant terms ($P < .05$). The random factor was never removed during model simplification. Parameterizing functions (3) and (5) required two steps: deriving a function describing the expected mean size at time $t + 1$ and a function describing the variance around mean size at time $t + 1$. For step 1, the predictors of mean size at time $t + 1$ were estimated using the model simplification procedure described before. Then, for step 2, the squared residuals of the minimal model of step 1 were fitted against a statistical function of the same form as in step 1 to estimate the variance in size at time $t + 1$. Following Easterling et al. (2000), the growth and inheritance functions (functions [3] and [5]) were then constructed using the following equation:

$$y_s = \frac{1}{\sqrt{2\pi}\sigma_s} e^{-(z' - \mu_s)^2/2\sigma_s^2}, \quad (3)$$

where y_s is either the growth or inheritance function of stage s , μ_s describes the mean effect of the predictors on growth or body size inheritance, and σ_s describes the squared residuals around μ_s . Binomial errors were used to estimate survival and transition probability, and Gaussian errors were used to estimate the other functions. Model assumptions on Gaussian errors and homoscedacity were confirmed by inspection of probability plots and error structures.

Stochastic Demographic Model

The stochastic demographic model was built using a two-state Markov chain that gives the probability distribution of environment states at time t . In this chain, state 1 is the good environment and state 2 is the bad environment, which results in the following Markov chain transition matrix $\mathbf{M}$ (Caswell 2001, p. 379):

$$\mathbf{M} = \begin{bmatrix} 1-p & q \\ p & 1-q \end{bmatrix}, \quad (4)$$

where p is the probability of switching from the good to

the bad environment and q is the probability of switching from the bad to the good environment. The serial or autocorrelation of the Markov chain equals $\rho = 1 - p - q$ (Caswell 2001, p. 379). High, positive values of ρ denote red noise; high, negative values of ρ denote blue noise; and $\rho = 0$ denotes white noise where the probability of switching states is independent of the current state. The temporal frequency at which the good environment occurs is given by $f = q/(p + q)$ (Caswell 2001, p. 379). In general, the stationary (long-term) mean of the environment is given by $fx_g + (1 - f)x_b$, where x_g and x_b respectively denote the values of the good and bad environments. The stationary variance of the environment is in turn given by $f(1 - f)(x_g - x_b)^2$, which shows that noise color does not affect the long-term variance of the environment. Here, the two environment states are categorical variables that affect the interpretation of the mean and variance of the environment. One could, for example, assign the arbitrary values of 1 and 0 to the good and bad environments, respectively, in which case the mean environment equals f and the variance $f(1 - f)$. By iterating $\mathbf{M}$, a time series of length $S = 3,000$ (with an initial transient length of 500 discarded, a starting population of one individual in each size bin, and the initial environment state chosen randomly; see also Tuljapurkar et al. 2003) was generated (an example of a stochastic run showing the stationary time series of the stage distribution is shown in the appendix: fig. A3). This sequence determines the environment state that a population experiences at each time step. If the state at time t is the good environment, the matrix approximation of the good-environment IPM is used, and conversely, the matrix approximation of the bad-environment IPM is used if the state at time t is the bad environment. In that way an IPM is generated at each time, which is stored with associated vectors of population structure for further analysis. Note that this procedure assumes that vital rates of one environment apply to mites that developed in the other environment. Note also that although we did not explicitly include population density as an explanatory variable in the character-demography functions, the good environment IPM can be considered density-independent as mites had ad lib. access to high-quality food. The bad-environment IPM on the other hand can be considered density dependent but only to some extent as, in reality, environment and population density do not necessarily fluctuate completely synchronously over time, in which case the stochastic sequences do not completely capture the density effect. This means that different stochastic sequences to a certain extent encompass situations in which the action of density dependence is captured in terms of temporal changes in environment states between time steps.

The long-run stochastic growth rate, λ_s , is calculated over a period of length S by taking the exponent of

$$\log(\lambda_s) = \frac{1}{S} \sum_{s=0}^{S-1} r_s, \quad (5)$$

with $r_t = \log[\sum_s \mathbf{p}_s(t+1) / \sum_s \mathbf{p}_s(t)]$ and $\mathbf{p}(t)$ is the population vector at time t . Lifetime reproductive success was calculated as the lifetime reproductive success averaged over $n = 50$ cohorts for each stochastic run:

$$R_0 = \frac{1}{n} \sum_{k=1}^n \sum_x l_k(x) m_k(x), \quad (6)$$

where $l_k(x)$ is the probability of surviving at least to age x in cohort k , and $m_k(x)$ is the average fertility of age class x in cohort k (cf. Tuljapurkar et al. 2009). Each stochastic run was divided into n/S intervals where the first cohort started life at the start of the first interval, the second at the start of the second interval, and so on. Average cohort generation time was calculated as before.

Perturbation Analysis

We first performed a deterministic perturbation analysis to each IPM to examine the elasticity of the population growth rate λ_0 when multiplying each parameter of each character-demography function by 1.001 (this increased positive parameters and decreased negative ones, and it is therefore important to note the sign of each parameter when interpreting the results). We then performed a stochastic elasticity analysis whereby we perturbed each character-demography function in both IPMs simultaneously to identify which functions under which stochastic regimes are most influential to the long-run stochastic population growth rate λ_s . Specifically, of each function of each IPM we consecutively perturbed the intercept, the linear coefficient (if it differed significantly from zero) and the quadratic coefficient (if it differed significantly from zero) by 0.1% and calculated the elasticity of λ_s to each function. The shape of a few character-demography functions differed between the two IPMs (appendix); in those cases only the most significant coefficient of each function was perturbed simultaneously in each IPM. The stochastic elasticity analysis was done such that each perturbation resulted in an increase in λ_s .

Results

Step 1: Model Performance

The first step in this investigation was to compare the fitted character-demography functions of the good- and bad-environment IPMs, which describe the associations between body size and survival, growth, and fertility for the

good and bad environments, respectively. This reveals that the shape and location of each function differed greatest between the two environment states for the adult life stage (fig. 1). Parameter values of each character-demography function are given in the appendix. We then verified that the IPMs were able to reproduce key population-level characteristics of the data. In general, the matrix approximations of the good- and bad-environment IPMs performed well in predicting life-history descriptors of mite populations at equilibrium (table 1). Individuals in the good environment have a high average fitness (λ_0), short generation time, high lifetime reproductive success and large body size, whereas individuals in the bad environment show the opposite characteristics (table 1).

Step 2: Perturbation Analysis

The deterministic perturbation analysis revealed that four character-demography functions are most influential to λ_0 : adult survival rate, adult fertility rate, tritonymph growth rate, and adult growth rate (figs. A4, A5). Of each of these functions, perturbation of the slope elicited the greatest change in λ_0 (except in case of fertility rate in the bad environment where the slope did not differ significantly from zero and so an intercept-only model was used of which the intercept was perturbed; fig. A4). We then performed the stochastic elasticity analysis by consecutively perturbing each character-demography function in both IPMs. This revealed that λ_s is always most elastic to either adult survival rate or fertility rate (fig. A6). Since slower life histories are characterized by increased sensitivity to changes in survival and faster life histories by increased sensitivity to changes in fertility (“Introduction”), we can equate the elasticity results of λ_s to the speed of life history and in that way match the different stochastic regimes we investigated to life-history speed (fig. 2). This reveals that slow life histories (where λ_s is most elastic to adult survival rate) are always favored when the autocorrelation ρ is high and negative (blue noise: top right corner of fig. 2). When $\rho = 0$ (white noise: along the antidiagonal in fig. 2), a slow life history is favored if $f < 0.50$, whereas a fast life history (where λ_s is most elastic to adult fertility rate) is favored if $f > 0.50$. When ρ is high and positive, a fast life history is favored when $f > 0.25$ (red noise: bottom left corner in fig. 2). Figure 2 also shows how λ_s and the distribution of adult body length vary across all stochastic environments (inset graphs in fig. 2).

Step 3: Do Different Life-History Variables Correlate with Environmental Change?

The third step of this investigation was to assess which life-history variables show a correlative response to

Table 1: Comparison between population biology quantities predicted by the good and bad environment integral projection models and those estimated directly from data

Quantity	Good environment		Bad environment	
	Predicted	Observed	Predicted	Observed
λ_0	1.41	1.25 ^a 1.13 ^b	1.08	NA
R_0	129.84	146.5 ^c 187.5 ^d	16.47	.00 ^c 8.95 ^e
σ_E	8.30	11.33 ^f	16.27	13.76 ^f
σ_L	30.69	37.46 ^f	29.91	29.40 ^f
σ_P	41.37	45.29 ^f	39.79	38.62 ^f
σ_T	92.70	48.19 ^f	35.75	34.43 ^f
σ_A	81.87	89.72 ^f	49.24	45.12 ^f
T	14.18	12.00 ^g 15 ^c	36.43	38.28 ^g 42 ^h
V	−3.50	−3.74 ^f	1.17	.13 ^f
$\bar{z}_E$	194.52	194.14 ^f	179.32	177.21 ^f
$\bar{z}_L$	219.29	231.82 ^f	212.02	210.37 ^f
$\bar{z}_P$	365.30	367.10 ^f	275.25	275.46 ^f
$\bar{z}_T$	465.63	508.47 ^f	317.93	318.34 ^f
$\bar{z}_A$	818.42	841.08 ^d	427.13	423.42 ^d

Note: The quantities are population growth rate (λ_0); mean body length ($\bar{z}$, μm) and standard deviation of body length (σ , μm) of eggs (E), larvae (L), protonymphs (P), tritonymphs (T), and adults (A); and generation time (T , days), strength of viability selection (V , μm), and mean lifetime reproductive success (R_0). The strength of viability selection was calculated as the difference in population-level mean body length after and before survival. Observed values of R_0 are calculated over a length of time that is equal to 1 generation time after maturation. Note that for convenience we refer to the filter paper diet as the bad environment even though on filter paper $\lambda_0 > 1$ and mite populations persist and do not decline. NA = not available.

^a Unpublished data.

^b Bulb mites on lily bulbs: Lesna et al. (1996).

^c Bulb mites on peanuts: Gerson et al. (1983).

^d Smallegange (2011a).

^e Smallegange and Coulson (2011).

^f This study.

^g Smallegange (2011b).

^h Gerson et al. (1983).

changes in noise color ρ and in good-environment-frequency f . For constant values of f , average fitness, that is, λ_s , increases with increasing ρ (going from blue to red noise), and for constant values of ρ , average fitness increases with increasing f (fig. 3A). Both generation time and lifetime reproductive success also increase with increasing ρ for constant values of f , but their increase is negligible (generation time) or minimal (lifetime reproductive success) for negative values of ρ (blue noise) and strong for high, positive values of ρ (red noise; fig. 3B, 3C). For constant values of ρ , generation time decreases and lifetime reproductive success increases with increasing f (fig. 3B, 3C). Mean adult body size decreases with increasing ρ for constant values of f , but this decrease is

Figure 2: Difference (Δ) in the elasticity of λ_s when perturbing adult survival rate and when perturbing adult fertility rate in relation to the probability of switching from the bad to good environment, q , and the probability of switching from the good to bad environment, p . The area below the $\Delta = 0$ line denotes where λ_s was most sensitive to perturbation of the fertility rate in both the good- and bad-environment IPMs, and the area above the $\Delta = 0$ line denotes where λ_s was most elastic to adult survival rate. The autocorrelation, ρ , in environmental regimes (denoted by the colored arrows) is red in the bottom-left corner, white along the antidiagonal, and blue in the top-right corner. The three dashed lines show values of p and q where the good-environment frequency f equals 0.25, 0.50, and 0.75. Along the latter three dashed lines, the variance of the environment equals 0.22, 0.50, and 0.22, respectively (if good and environment are valued at 1 and 0, respectively). For each of five combinations of noise color and f , a set of three inset graphs give an example stochastic run (bottom graph of each set), the associated change in population growth rate (middle graph of each set), and the size distribution of adults (top graph of each set) at two points along the stochastic run (denoted by the black and gray arrows in the middle graph of each set, which correspond to the black and gray size distribution in the top graph of each set). One stochastic run was performed for each point in the figure.

Figure 3: The stochastic growth rate λ_s (A), generation time (days; B), lifetime reproductive success (number of eggs produced; C), and mean adult body size (μ m; D) as a function of the autocorrelation ρ of environmental regimes. Also shown is the fitness landscape: the stochastic growth rate in relation to generation time (E), lifetime reproductive success (F), and mean adult body size (G). Symbols indicate three values of f , the good-environment frequency: 0.25 (squares), 0.50 (triangles), and 0.75 (diamonds). In E–G, the size of these symbols increases with increasing autocorrelation (ρ) in the environmental regimes: small symbols denote blue noise (negative ρ), intermediately sized symbols denote white noise ($\rho = 0$), and large symbols denote red noise (positive ρ). The range of noise colors is larger for $f = 0.50$ than for other values of f (see fig. 2).

minimal when ρ is negative (blue noise) and maximal when ρ is high and positive (red noise; fig. 3D). For constant values of ρ , mean adult body size increases with increasing f (fig. 3D). These results show that average fitness, generation time, lifetime reproductive success, and body size all show a correlative response to changes in good-environment frequency (fig. 3A–3D). In response to a change in noise color, however, only average fitness shows a correlative response across the whole color spectrum, whereas generation time, lifetime reproductive success, and body size only show a correlative response if noise shifts occur in red environments (fig. 3A–3D).

Step 4: Indicators of Fitness and Life-History Speed

For step 4 we explored which quantities correlate with average fitness with changing noise color and good-environment frequency. This revealed that generation time and average fitness are negatively correlated as f increases (keeping ρ constant; fig. 3E). As ρ increases (keeping f constant), generation time and average fitness are positively correlated under red noise but uncorrelated under blue noise (fig. 3E). Lifetime reproductive success and average fitness correlate positively as f increases (keeping ρ constant; fig. 3F). They also correlate positively as ρ increases (keeping f constant), but average fitness values level off at high levels of lifetime reproductive success under red noise, especially at high levels of f (fig. 3F). This means that under red noise, for each f , there is a range of values of lifetime reproductive success at which average fitness is at a maximum. Mean adult body size and average fitness correlate positively as f increases (keeping ρ constant) but negatively as ρ increases (keeping f constant), except in the bluest environments when $f = 0.75$ and where body size and average fitness are uncorrelated (fig. 3G). To summarize, generation time, lifetime reproductive success, and body size inform on how average fitness changes with changing good-environment frequency, but no single quantity informs on how average fitness responds to changes in the environmental autocorrelation across the whole spectral gradient.

Finally, we explored if average fitness, generation time, or lifetime reproductive success correlate with life-history speed, that is, the slow and fast life-history patterns identified in figure 2 (body size is excluded as the covariation between maturation, longevity, and fecundity along the slow-fast life-history speed continuum is defined for a given body mass; Stearns 1983; Gaillard et al. 1989). To this end, we scaled the stochastic elasticities of λ_s to adult survival rate and fertility rate so that they sum to one. This means that if the scaled elasticity of λ_s to adult survival rate is greater than 0.5, λ_s is most sensitive to changes in adult survival rate and a slow life history exists. Conversely,

a fast life history exists if the scaled elasticity of λ_s to adult survival rate is smaller than 0.5 (in which case λ_s is most sensitive to changes in fertility rate). Across all stochastic regimes, i.e. across all values of f and ρ , faster life histories are associated with higher average fitness, shorter generation time, and higher lifetime reproductive success (gray symbols in fig. 4). These results are qualitatively similar to the deterministic outcome (table 1) and to established classifications of fast and slow life histories (Stearns 1983; Gaillard et al. 1989). Of the three quantities, average fitness and lifetime reproductive success correlate best with the speed of life history (fig. 4A, 4C). Both these quantities show much less variation in response to environmental change than generation time (fig. 4B). Because variation in generation time is so high, the range of values that are associated with both fast and slow life histories is large compared to the total range of their observed values (fig. 4B). Therefore, generation time can be considered a poor predictor of the speed of life history in stochastic environments. The likely reason that generation time shows such large variation across environments is that this quantity displays opposite correlative responses to increasing ρ and f : generation time increases with increasing ρ but decreases with increasing f (fig. 4B; see also fig. 3E). Average fitness and lifetime reproductive success, on the other hand, show the same correlated response to increasing ρ and f : both quantities increase with increasing ρ and f (fig. 4A, 4C; see also fig. 3F) and, as a result, vary less across stochastic regimes.

Discussion

Using recently developed structured models and tools from stochastic demography, we explored how different life-history variables vary in response to environmental change. Several insights were gained. First, our graphical analyses revealed that life-history speed can be shaped by both the temporal frequency of favorable environment states and the patterning of environment states through time. In constant environments, life-history variables such as age at maturity and generation time provide a measure of the position of a given population along the slow-to-fast life-history continuum (Charlesworth 1994; Heppell et al. 2000; Oli and Dobson 2003; Gaillard et al. 2005; Stahl and Oli 2006). Our analysis revealed that in stochastic environments, lifetime reproductive success and population growth rate are reliable proxies for life-history speed. Generation time, on the other hand, seems a less reliable proxy as its direction of change in response to environmental change depends on whether the frequency of good environments or the serial correlation in environment states is changing.

Second, we showed that, as the frequency of favorable

Figure 4: The scaled elasticity λ_s to perturbation of adult survival rate as a function of stochastic growth rate (A), generation time (B), and lifetime reproductive success (C). The black symbols represent three values of f , the good-environment frequency: 0.25 (squares), 0.50 (triangles), and 0.75 (diamonds). The size of these symbols increases with increasing autocorrelation (ρ) in the environmental regimes: small symbols denote blue noise, intermediately sized symbols denote white noise, and large symbols denote red noise. In gray are values associated with all environmental regimes explored in this study, that is, all combinations of the probability of switching from the bad to good environment, q , and the probability of switching from the good to bad environment, p (fig. 2). The horizontal dashed lines denote where the scaled elasticity of λ_s equals 0.5: values above this line correspond to a slow life history, and values below this line correspond to a fast life history. Calculating generation time as $(1/n) \sum_{k=1}^n \sum x_k(x) m_k(x) / R_0$ (cf. Tuljapurkar et al. 2009) reveals the same pattern as in B.

environment states changes and as noise color shifts between white and red environments, different quantities can change together in a consistent and predictable way: regardless of the type of environmental change, average fitness and lifetime reproductive success always correlate positively, whereas generation time and body size always correlate negatively. However, the relationship between average fitness/lifetime reproductive success and generation time/body size depends on the type of environmental

change. Furthermore, with a decrease in environmental quality due to a decrease in good-environment frequency or a shift from red to white environments, average fitness and lifetime reproductive success always decrease, but the response of generation time and body size depends on which type of stochastic change drives the environmental deterioration. We also showed that different quantities—generation time, lifetime reproductive success, and body size—can inform on how average fitness responds to a

change in the temporal frequency of favorable environment states. However, no predictors on how average fitness changes along the full spectral gradient were identified. Recent work indicates that the color of temperature-climate variables has become less red-shifted, at least on a continental scale (García-Carreras and Reuman 2011), and it is therefore of interest to investigate correlates of the change in average fitness for this shift along the color gradient. Climate variability increases as climate variables become less red (this is because the temporal frequency with which environmental conditions change increases), and theory states that increased variability of demographic rates decreases the stochastic population growth rate (Lewontin and Cohen 1969; but see Drake 2005). This is indeed what we found with our graphical analysis.

To what extent the above results can be generalized to other species depends foremost on whether the character-demography functions that form the basis of our analyses are similar to those of other species. A (nonexhaustive) review of published IPMs reveals that the shape of the bulb mite character-demography functions are comparable to those of other species (e.g., Soay sheep *Ovis aries* (Coulson et al. 2010); soil mite *Sancassania berlesei* (Ozgul et al. 2012); Nile crocodile *Crocodylus niloticus* (Wallace et al. 2012), except for the survival rate of adults in the bad environment as this is of an atypical hump shape (fig. 1). We therefore reran our analyses, setting the adult survival rate in the bad environment equal to the juvenile survival rate in the bad environment, which we considered a suitable, biologically realistic alternative. This revealed that noise color had little influence on any of the life-history variables but the life-history response to changes in good-environment frequency was the same as before (fig. A7). Importantly, lifetime reproductive success and population growth rate remain reliable proxies for life-history speed, and because variation in life-history variables is mainly determined by variation in good-environment frequency, generation time now also reliably informs on life-history speed (fig. A8). Thus, altering the shape of adult survival rate in the bad environment has no effect on the life-history response to changes in good-environment frequency or on the reliability of population growth rate and lifetime reproductive success as indicators of life-history speed. These are therefore results that may be generalized to other species with similar vital rates.

There are several ways to characterize environmental change. This can be a change in mean environment, in environmental variance, in the serial correlation of environment states (noise color), or in the frequency of favorable environment states. Here we focused on the latter two characteristics by changing the parameters p and q , which determine the probabilities of switching between environment states. However, changing the frequency of

favorable environment states changes both the mean environment and environmental variance at the same time, which means that their effects cannot be separated. An alternative way that could be adopted in future studies to investigate the population response to changes in the mean environment and environmental variance using IPMs, is by altering the parameter estimates of the character-demography functions and their variance. Coulson et al. (2011) applied this approach to the character-demography functions of Yellowstone gray wolves and concluded from the wide range of expected population change that detailed knowledge on how the environment affects growth, survival, and reproduction of individuals of different life stages, genotypes, and so forth is required for an accurate prediction of the response of populations to environmental change. Here, we made a first step toward identifying reliable predictors of life-history change by analyzing demographic data that were obtained under controlled laboratory circumstances. Several predictors of the life-history response of populations to changes in the environment were identified. However, unlike Coulson et al. (2011), we did not explicitly include population density as an explanatory variable in the character-demography functions, and it would therefore be interesting to investigate whether the patterns found in this study hold when density dependence is explicitly included in the population models.

Finally, confirming the reliability of our results requires that our predictors of the life-history response are tested in a population experiment. This experiment can then also be used to test a crucial assumption of this study that environmental noise color tinges the dynamics of populations. Population studies on ciliates, for example, suggest that internal mechanisms redden population dynamics rather than the noise color of external environmental variables (Petchey 2000; Laakso et al. 2003). Yet, a study on flour beetles found that under some dynamical regimes, population power spectra can be tinged blue by external environmental variables that show blue noise (Reuman et al. 2008). This experimental test can also shed light on the links between environmental change and variability in demographic rates (e.g., Coulson et al. 2001; Drake 2005) as environmental variability sometimes does not translate into variability in demographic rates due to buffering (Pfister 1998; Morris and Doak 2004) or environmental canalization (Gaillard and Yoccoz 2003). It should also be pointed out that our approach does not accommodate potentially important effects of environmental change at the individual level, such as bet-hedging strategies (Seger and Brockmann 1987) and any delayed effects of previously experienced environmental conditions on future development. Experiments should also be conducted to test the assumption that vital rates of one environment apply to mites that developed in the other environment holds.

This assumption likely holds if functions are similar and body size distributions of individuals in different environments overlap, which was the case here for most juvenile vital rates. Adult survival and fertility rate, however, differed greatly between environments, and adult body size distributions showed little overlap. In case of adult survival, extrapolating survival rates likely poses few problems. Large adult females from the good environment that suddenly experience bad environmental conditions would be unable to obtain enough resources to meet their maintenance and reproduction costs and therefore would have very low survival rates in the bad environment, which matches the extrapolated survival rate of the bad environment to large body sizes. Vice versa, small adults from the bad environment that move to the good environment would experience an increase in survival rate as now ample food is available. In case of fertility rate, there likely is a discrepancy between extrapolated functions and actual fertility patterns. In the bad environment, large adults from the good environment will for a short while still have a high production rate of eggs, as these were already produced in the good environment and this would introduce a reproduction lag. Small adults in the good environment, on the other hand, would never be able to reach the high levels of egg production achieved by much larger females. To what extent and under which environmental regimes these extrapolation errors would create a substantial mismatch between our predictors of the life-history response and actual life-history patterns remains to be tested.

Acknowledgments

We thank S. Schindler for discussions and her help with the cohort calculations. This work is sponsored by an ERC Advanced Grant awarded to T.C.

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