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Population Responses to Perturbations: The Importance of Trait-Based Analysis Illustrated through a Microcosm Experiment

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ABSTRACT: Environmental change continually perturbs populations from a stable state, leading to transient dynamics that can last multiple generations. Several long-term studies have reported changes in trait distributions along with demographic response to environmental change. Here we conducted an experimental study on soil mites and investigated the interaction between demography and an individual trait over a period of nonstationary dynamics. By following individual fates and body sizes at each life-history stage, we investigated how body size and population density influenced demographic rates. By comparing the ability of two alternative approaches, a matrix projection model and an integral projection model, we investigated whether consideration of trait-based demography enhances our ability to predict transient dynamics. By utilizing a prospective perturbation analysis, we addressed which stage-specific demographic or trait-transition rate had the greatest influence on population dynamics. Both body size and population density had important effects on most rates; however, these effects differed substantially among life-history stages. Considering the observed trait-demography relationships resulted in better predictions of a population's response to perturbations, which highlights the role of phenotypic plasticity in transient dynamics. Although the perturbation analyses provided comparable predictions of stage-specific elasticities between the matrix and integral projection models, the order of importance of the life-history stages differed between the two analyses. In conclusion, we demonstrate how a trait-based demographic approach provides further insight into transient population dynamics.

Keywords: integral projection model, matrix population model, *Sancassania berlesei*, soil mite, trait-based demography, transient perturbation analysis, transient population dynamics.

Introduction

The recognition of the ubiquity of environmental variation has led to the largest advances in our understanding of

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population biology; we now recognize that environmental variation radically affects both population and evolutionary dynamics (Tuljapurkar 1990; Lundberg et al. 2000; Bjornstad and Grenfell 2001; Ruokolainen et al. 2009). Population dynamics are rarely stable but instead consist of a sequence of perturbations away from an attractor. Each perturbation is followed by transient dynamics as the system reapproaches the attractor before it is perturbed again. Thus, an understanding of the dynamics of populations in variable environments consequently requires an understanding of the transient dynamics (Hastings 2001, 2004). This is true both in the short term, when predicting how a population may respond numerically to a particular perturbation, and in the long term, as the perturbations may alter the selection pressures on the life history, leading to evolutionary change (Coale 1972; Benton and Grant 1999b; Fox and Gurevitch 2000; Koons et al. 2006; Caswell 2007; Tuljapurkar et al. 2009; Ezard et al. 2010).

The significance of transient dynamics for a particular system will depend on the strength of the perturbations and the population's demographic resilience to them. Studies that have followed individuals over multiple generations have provided detailed accounts of species' demographic responses to short- and longer-term perturbations (Walther et al. 2002; Parmesan 2006). Interestingly, some of these studies have reported simultaneous changes in phenotypic traits, such as body size, along with the observed changes in population dynamics (e.g., Reznick and Endler 1982; Coltman et al. 2003; Reale et al. 2003). Similarly, census-based studies often report variability in both demographic rates and traits over time, whether in the lab (Benton and Beckerman 2005) or in the field (Genner et al. 2010). In most cases where perturbations induce a significant phenotypic change within relatively few generations, the observed response has been attributed to phe-

notypic plasticity rather than a selection-based evolutionary response (Ozgul et al. 2009, 2010; Plaistow and Benton 2009). Regardless of the underlying ecological or evolutionary processes, such changes in individual trait distributions can be intimately linked to changes in population dynamics (Pelletier et al. 2007).

The observations of simultaneous demographic and phenotypic changes suggest that studying trait dynamics can provide further insight into the mechanisms underlying the demographic response to environmental perturbations. Both theoretical and empirical approaches have shown how the distribution of individual traits can change depending on resource levels and population density (Grimm and Uchmanski 2002; Ozgul et al. 2009) and how population dynamics in turn are influenced by trait dynamics (Uchmanski 2000; Ovadia and Schmitz 2002; Ozgul et al. 2010). Theoretical approaches have provided evaluation of model predictions with and without consideration of individual variability (Grimm and Uchmanski 2002; Pfister and Stevens 2003), and a few exemplary studies have empirically investigated demographic consequences of individual variation in traits (Ovadia and Schmitz 2002; Filin et al. 2008). Although individual variation has been shown to influence several aspects of population dynamics, the ability of a trait-based demographic approach to predict a population's response to perturbations has yet to be tested empirically.

The transient population dynamics can be further complicated by density dependence. If the nonlinearity induced by density dependence is strong enough, then the transient phase usually lasts much longer and more substantial changes in the dynamics are observed (Hastings and Higgins 1994). Despite the substantial effect of density dependence on transient dynamics, most population models often assume no or only very basic forms of density dependence that may overlook the underlying processes (Grant and Benton 2000). A more mechanistic account of density dependence can be achieved by focusing on an intermediate trait, such as body size, that is directly affected by density and environment and, in turn, differentially affects survival and reproduction at each stage. Such an approach can also account for the effect of these factors on the transition of the focal trait, such as trait development over different stages (i.e., physiological growth) or passing on the trait to offspring generation (i.e., offspring body size), which can show differential response to perturbations.

Traits such as body size have been incorporated in population analyses, using a diverse set of population models with assumptions of various forms of variation among individuals. Widely used matrix population models (MPMs; Tuljapurkar and Caswell 1997; Caswell 2001) can group individuals into multiple trait classes; however, because of coarsely defined trait categories, they do not allow subtle changes in trait distributions and resulting changes in demography to be investigated. Physiologically structured population models (PSPMs), on the other hand, have been used to study the mechanistic feedback between resources, physiological traits, and population dynamics (Metz and de Roos 1992). Earlier PSPMs accounted for between-cohort but not within-cohort variation in individual traits, which is ubiquitous in nature. Individual heterogeneity is one of the defining features of individual-based modeling approaches (IBMs; Grimm and Railsback 2005), which can easily be tailored to incorporate individual traits as state variables (e.g., Grimm and Uchmanski 2002; Ovadia and Schmitz 2002; Filin et al. 2008). Recent individual-based adaptations of PSPMs (de Roos et al. 2009; Gonzalez-Suarez et al. 2011) relax the strong assumption of the PSPM framework by allowing within-cohort variation in individual traits. However, because all individual-based models include demographic stochasticity by default, the comparison of their analytical perturbations (e.g., sensitivity and elasticity analyses) to those of basic modeling approaches is not straightforward. Another modeling approach, integral projection models (IPMs), addresses these shortfalls (Easterling et al. 2000; Ellner and Rees 2006; Coulson et al. 2010). IPMs project the distribution of a continuous trait on the basis of demographic and trait-transition functions and allow for modeling of changes in both the distribution of traits and the number of individuals. An IPM can be approximated as an MPM and includes only the trait dynamics as an additional factor, and its predictions are not confounded by demographic stochasticity. As such, it allows comparable analytical insight to the MPM.

For most species living in the wild, collecting individual-based morphological and demographic data that span several generations requires years if not decades of fieldwork. Furthermore, general inferences on intra- or interspecific comparisons are difficult to make because of lack of control over the variation in external factors. For these reasons, laboratory microcosms, which allow for monitoring of several generations in short time periods and effective control of external factors, provide ideal systems for investigating trait, demography, and environment interactions. Studies on laboratory populations of one such species, soil mites *Sancassania berlesei*, have provided important insights into stochastic demography in general and density-dependent and density-independent processes in particular (Benton and Beckerman 2005). Previous studies on soil mites have revealed a complex interaction among density, food availability, parental effects, demographic rates, and population dynamics (Beckerman et al. 2002, 2006; Benton and Beckerman 2005; Plaistow et al. 2007). Soil mite life history is highly plastic with respect
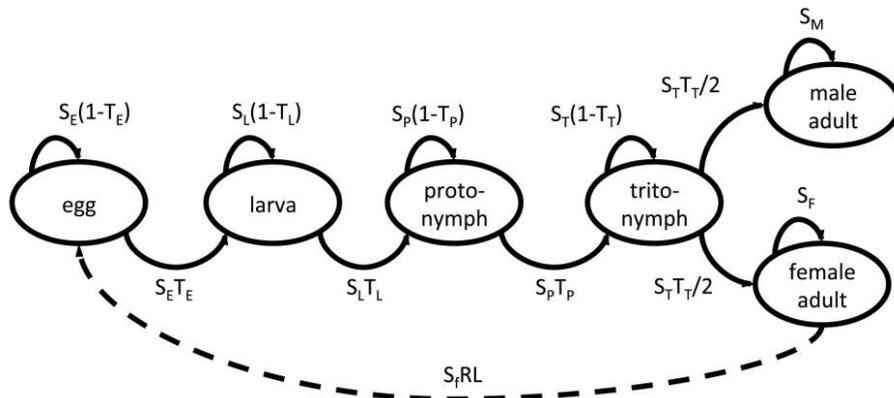
Figure 1: Life-cycle graph for the soil mite, with six life-history stages: egg (*E*), larva (*L*), protonymph (*P*), tritonymph (*T*), adult male (*M*), and adult female (*F*). S_x is the survival probability of an individual in stage *x*, T_x is the probability of an individual in stage *x* moving to the next stage conditional on survival, *R* is the probability of reproducing, and *E* is the number of eggs per reproducing female. All rates are per day.

to resource availability, which is a function of food supply and population density. By varying the food supply, one can induce environmental perturbations and observe transient dynamics (Benton et al. 2004). A previous attempt to fit MPM to data on transient dynamics failed to capture the way in which the system responded to perturbations. A plausible reason for this lack of fit is that an MPM did not incorporate the trait-based dynamics that occurred within each stage.

Here we conducted an individual-based study of soil mites and investigated the interaction between demography and individual traits over a transient period of nonstationary dynamics. By following individual fates and body sizes at each life-history stage, we first investigated how body size and population density influenced demographic rates. Next, by comparing two alternative modeling approaches, a density-dependent matrix projection model and a density-dependent integral projection model, we investigated whether consideration of trait-based demography enhanced our ability to predict transient dynamics. Finally, by utilizing a prospective perturbation analysis, we addressed which stage-specific demographic or trait-transition rates had the greatest influence on population dynamics and how these parameter elasticities varied among different density levels.

Methods

Species

We parameterized two population models (MPM and IPM), using individual-based demographic and phenotypic trait data collected during a 6-week experiment on

soil mites *Sancassania berlesei*. The population used in this experiment originates from a laboratory culture originally collected in 2005 in Aberdeenshire, United Kingdom, from an agricultural chicken manure pellet heap. Details regarding the biology of the species, the maintenance of the stock culture, and basic experimental techniques can be found elsewhere (Benton and Beckerman 2005).

Density-Dependent Model (MPM)

First we conducted an analysis of population dynamics without considering trait dynamics. To account for the previously described stage-specific differences in demographic rates (Benton and Beckerman 2005), we parameterized a two-sex, density-dependent, stage-structured matrix model:

$$\begin{bmatrix} S_E(d)T_E'(d) & 0 & 0 & 0 & 0 & S_F(d)R(d)F(d) \\ S_E(d)T_E(d) & S_L(d)T_L'(d) & 0 & 0 & 0 & 0 \\ 0 & S_L(d)T_L(d) & S_P(d)T_P'(d) & 0 & 0 & 0 \\ 0 & 0 & S_P(d)T_P(d) & S_T(d)T_T'(d) & 0 & 0 \\ 0 & 0 & 0 & S_T(d)T_T(d)/2 & S_M(d) & 0 \\ 0 & 0 & 0 & S_T(d)T_T(d)/2 & 0 & S_F(d) \end{bmatrix},$$

where *d* is the population density weighted by the body size in each stage, $S_i(d)$ is the probability of an individual in stage *i* surviving to the next day, $T_i(d)$ is the probability of transition—or no transition, $T_i'(d)$—to the next stage conditional on survival, $R(d)$ is the probability of an adult female reproducing, and $F(d)$ is the number of eggs produced by each reproducing female. The corresponding population vector includes the number of individuals in each of the six life-history stages: egg, larva, protonymph, tritonymph, adult male, and adult female (fig. 1). Each of the demographic rates in the projection matrix is a func-

tion derived from the most parsimonious models that include weighted density but not body size as explanatory factors (tables A1–A4, which are available online in a zip file). We assumed a postbreeding census such that births occur just before the census (Caswell 2001). Because different stages were expected to have different contributions to the density effect, the weighted population density was estimated as the sum of products of average log-body size and number of individuals in each stage. Egg stage was excluded from weighted density estimation.

Using the initial stage distribution as the starting population vector, we projected the number of individuals in each stage for 100 days. A 6 × 6 matrix was parameterized on the basis of the estimated weighted population density for each time step and was used in an iterative matrix multiplication to project the population vector to the next time step.

Density- and Trait-Dependent Population Model (IPM)

Next, using the most parsimonious functions (explained below) to relate body size and weighted density to each demographic and trait-transition rate, we constructed a two-sex, density-dependent, size- and stage-structured integral projection model (IPM) that would allow modeling of changes in both the phenotypic trait distribution and the population structure (Easterling et al. 2000; Ellner and Rees 2006; Coulson et al. 2010).

The IPM tracks the distribution of body size in each stage. For a general stage class i, the number of individuals in the size range $[x, x + dx]$ at time t is denoted by $n_i(x, t)$. The dynamics of $n_i(x, t)$ are governed by a set of coupled integral equations:

$$n_\mathrm{E}(y, t+1) = \int_\Omega S_\mathrm{F}(x, d)R(x, d)F(x, d)\beta(y|x, d)n_\mathrm{F}(x, t)dx$$

$$+ \int_\Omega S_\mathrm{E}(x, d)T'_\mathrm{E}(x, d)\alpha_\mathrm{E}(y|x)n_\mathrm{E}(x, t)dx,$$

$$n_\mathrm{L}(y, t+1) = \int_\Omega S_\mathrm{E}(x, d)T_\mathrm{E}(x, d)\alpha_\mathrm{E}(y|x, d)n_\mathrm{E}(x, t)dx$$

$$+ \int_\Omega S_\mathrm{L}(x, d)T'_\mathrm{L}(x, d)\alpha_\mathrm{L}(y|x, d)n_\mathrm{L}(x, t)dx,$$

$$n_\mathrm{P}(y, t+1) = \int_\Omega S_\mathrm{L}(x, d)T_\mathrm{L}(x, d)\alpha_\mathrm{L}(y|x, d)n_\mathrm{L}(x, t)dx$$

$$+ \int_\Omega S_\mathrm{P}(x, d)T'_\mathrm{P}(x, d)\alpha_\mathrm{P}(y|x, d)n_\mathrm{P}(x, t)dx,$$

$$n_\mathrm{T}(y, t+1) = \int_\Omega S_\mathrm{P}(x, d)T_\mathrm{P}(x, d)\alpha_\mathrm{P}(y|x, d)n_\mathrm{P}(x, t)dx$$

$$+ \int_\Omega S_\mathrm{T}(x, d)T'_\mathrm{T}(x, d)\alpha_\mathrm{T}(y|x, d)n_\mathrm{T}(x, t)dx,$$

$$n_\mathrm{M}(y, t+1) = \int_\Omega \frac{S_\mathrm{T}(x, d)T_\mathrm{T}(x, d)\alpha_\mathrm{T}(y|x, d)n_\mathrm{T}(x, t)dx}{2}$$

$$+ \int_\Omega S_\mathrm{M}(x, d)\alpha_\mathrm{M}(y|x, d)n_\mathrm{M}(x, t)dx,$$

$$n_\mathrm{F}(y, t+1) = \int_\Omega \frac{S_\mathrm{T}(x, d)T_\mathrm{T}(x, d)\alpha_\mathrm{T}(y|x, d)n_\mathrm{T}(x, t)dx}{2}$$

$$+ \int_\Omega S_\mathrm{F}(x, d)\alpha_\mathrm{F}(y|x, d)n_\mathrm{F}(x, t)dx,$$

where Ω is a closed interval characterizing the size domain and d is the weighted population density at time t. For an individual of size x to remain in the population, it must survive to the next day, either stay in the same stage or move to the next stage, and then grow to size y. Consequently, the survival-growth component of the IPM includes the density-dependent survival $S_i(x, d)$, transition $T_i(x, d)$ (or no transition $T'_i = 1 - T_i$), and growth $\alpha_i(y|x, d)$ functions for each stage. Eggs do not grow, hence $\alpha_\mathrm{E}(y|x) = 1$. For an adult female to contribute an egg to the population the next day, it must survive and successfully reproduce eggs, the number and size of which depends on the female's size x. Consequently, the recruitment component of the IPM includes the density-dependent survival $S_\mathrm{F}(x, d)$, reproduction $R(x, d)$, egg number $F(x, d)$, and egg size $\beta(y|x, d)$ functions, all of which are dependent on the size of the adult female x and the weighted population density d.

The growth kernel $\alpha_i(y|x, d)$ gives the conditional distribution of attained body size y at time $t + 1$ given size x and population density d at time t, whereas the egg size kernel $\beta(y|x, d)$ gives the conditional distribution of produced egg size y at $t + 1$ given adult female size and population density d at time t. The two kernels are derived from the demographic growth $G_i(x, d)$ and egg size $E(x, d)$ models, respectively. We assumed that a tritonymph making the transition to an adult stage is equally likely to become a male or a female.

The survival-growth and recruitment components were used for discrete approximation of the IPM at a set of size classes defined by "mesh points" for each stage. For each size class, the transition rate was estimated at the midpoint of the two mesh points. The numerical accuracy of the

approximation increases with the number of mesh points (Ellner and Rees 2006). We divided the body size interval into 50 size classes for each life-history stage, as this ensured that the population growth rate calculations were accurate to at least three decimal places.

Using the initial body size × stage distribution as the starting population vector, we projected the stage and size distribution for 100 days. A 300 × 300 matrix (including 50 size classes × 6 stages) was parameterized on the basis of the estimated weighted population density for each time step and, similar to the MPM, it was used in an iterative matrix multiplication to project the population vector to the next time step.

Prospective Perturbation Analysis of the Density-Dependent IPM and MPM

To identify the relative influence of demographic and trait-transition functions on population dynamics, we implemented a prospective perturbation analysis and investigated the proportional change in λ in response to proportional changes in each of the demographic and trait-transition rates (i.e., elasticities) evaluated at different densities. To understand how much including trait dynamics alters our understanding of demographic sensitivities, we compared the elasticities of IPM and MPM. We parameterized the MPM and the IPM for 23 weighted density levels between 80 and 320, and at each level we iterated the model by multiplying one of the focal vital or trait-transition rate by 1.005. We assumed zero covariance among vital and trait-transition rates. Because these are lower-level elasticities and give the proportional change in λ in response to a 0.5% change in each lower-level parameter, they do not necessarily add up to 1. The elasticity of λ to changes in each of the demographic and trait-transition rates was evaluated by comparing the proportional changes in λ at each weighted density level.

Experimental Design

We conducted a 6-week experiment to parameterize the two population models. A sample population and a control population were set up, using existing lab populations that have been fed on a constant feeding regime for the past 3 years and therefore have adapted to experimental conditions. Before setup, half of the females were removed from each population and fed a high-food diet for 7 days in order to increase fecundity. On the day of setup (i.e., day 1), the large fecund females were reintroduced to the original populations and both populations were rehoused in new tubes. The populations were initially fed on two balls of yeast, which was the original feeding regime, for 7 days. Food amount was then reduced to 1.5 balls in

powdered form on day 8. The aim of increasing female fecundity and then reducing resources was to promote perturbation of the populations and trigger nonstationary transient dynamics (Beckerman et al. 2003). This also creates a mismatch between phenotype, current, and past environments. Population dynamics, stage structure, and life-history traits were then monitored over 6 weeks.

For both tubes, the number of individuals at each of the six stages was counted under microscopy every morning, Monday through Friday. High-resolution (2,560 × 1,920 pixels), low-magnification (×1 zoom mag through a ×1 HR plan Apo) photographs of both tubes were taken; from these photographs, 20 individuals of each stage were identified and measured for body size. Photographs were taken using a Nikon DS-5M camera mounted on a Nikon SMZ1500 stereo microscope. The camera was controlled by a Nikon DS-U1 connected to a PC using Nikon Elements Dv2.3. Body size was measured as the distance from the tip of the hypostome to the tip of the opisthosoma. Populations were fed after the photographs were taken, at 1000 hours each day, Monday through Sunday.

From one tube, the "sample tube," individuals were sampled daily after 1300 hours (as the food provided had been consumed by 1200 hours). Twenty tubes were set up, each containing a larva, a protonymph, a tritonymph, and an adult male and female. Additionally, five extra tubes were set up that included an adult male and an adult female. These individual tubes were then photographed at high magnification for body size. Sampling occurred Monday, Wednesday, and Friday.

Sampled individuals were rephotographed on the following day and then checked for survival and stage transition. Body-size measurements were taken to measure daily growth, and eggs that had been laid were counted and measured. Eggs were monitored for 7 days for hatching. Eggs that did not hatch by the seventh day were considered dead. The sampled individuals were returned to the population before the population was fed, and they were included in the total population counts.

The experiment described above could not follow the egg-size to larva-size transition, as the produced eggs were not individually separated from each other. We conducted a separate experiment to look at the relationship between egg size and larva size. Adult females were taken from a variety of experimental tubes (constant and variable treatments) and isolated in individual tubes where yeast was provided. Individual eggs were collected, placed in small vials, and measured for size. The vials were monitored twice daily until the eggs hatched. When the eggs hatched, the larva sizes were measured as described above.

Table 1: Models Describing the Stage-Specific Demographic and Trait-Transition Rates

Rate, model	Fitted GLM/GAM	n
Survival:		
$\text{Logit}(S_E)$	$3.17_{(.16)} + f(x^*, d^*, \text{df} = 4.61)$	274
$\text{Logit}(S_L)$	$55.31_{(38.81)} - 9.63_{(7.03)}\, x - .15_{(.18)}\, d^* + .03_{(.03)}\, xd$	245
$\text{Logit}(S_P)$	$-28.44_{(43.37)} + 5.47_{(7.42)}\, x - .15_{(.17)}\, d^* - .03_{(.03)}\, xd$	273
$\text{Logit}(S_T)$	$2.99_{(.31)} + f(x^*, d, \text{df} = 4.14)$	273
$\text{Logit}(S_M)$	$3.38_{(21.37)} + .01_{(3.38)}\, x - .003_{(.003)}\, d$	353
$\text{Logit}(S_F)$	$-3.64_{(18.24)} + .93_{(2.80)}\, x - .001_{(.002)}\, d$	354
Transition:		
$\text{Logit}(T_E)$	$.44_{(.002)} + f(x^*, d^*, \text{df} = 7.97)$	266
$\text{Logit}(T_L)$	$-5.82_{(1.82)} + f(x^*, \text{df} = 1.68) + f(d, \text{df} = 1)$	226
$\text{Logit}(T_P)$	$-4.70_{(.96)} + f(x^*, \text{df} = 1.97) + f(d, \text{df} = 1)$	250
$\text{Logit}(T_T)$	$-179.8_{(23.86)} + 28.76_{(3.83)}\, x^* + .001_{(.002)}\, d$	256
Reproduction:		
$\text{Logit}(R)$	$-75.17_{(16.91)} + 11.94_{(2.62)}\, x^* - .01_{(.002)}\, d^*$	354
Egg number:		
$\log(\text{E}(L))$	$1.29_{(.03)} + f(x^*, d^*, \text{df} = 5.50)$	305
Growth:		
G_E	$5.32_{(.01)} + f(x^*, \text{df} = 1.58)$	44
G_L	$5.53_{(.004)} + f(x^*, d^*, \text{df} = 4.49) + .04_{(.01)}\, \Upsilon^*$	225
G_P	$5.87_{(.004)} + f(x^*, d^*, \text{df} = 4.41) + .02_{(.01)}\, \Upsilon^*$	250
G_T	$6.21_{(.004)} + f(x^*, d^*, \text{df} = 4.39) + .03_{(.07)}\, \Upsilon^*$	253
G_M	$1.14_{(.16)} + .81_{(.02)}\, x^* + .00008_{(.00002)}\, d^*$	332
G_F	$6.58_{(.002)} + f(x^*, d^*, \text{df} = 4.81)$	322
Egg size:		
E	$4.94_{(.28)} + .04_{(.04)}\, x - .00003_{(.00002)}\, d$	279

Note: The models include the main effects of log-size x, weighted population density d, their interaction effect xd, and stage transition Υ. In the model identifiers, subscript letters indicate the six stages, as follows: E, egg; L, larva; P, protonymph; T, tritonymph; M, adult male; F, adult female. Subscript numerical values are standard errors of parameter estimates. The function $f(x, \text{df})$ is a standard tensor product-smoothing function of x with the given degrees of freedom (df). An asterisk indicates significance (at $\alpha = 0.05$) of each term, based on the likelihood ratio comparison with the reduced models. n is the corresponding sample size. $\text{Logit}(Y)$ indicates binomial regression using logit link, whereas $\log(\text{E}(Y))$ indicates Poisson regression using log-transformed expected values. Detailed model-comparison tables for each demographic and trait-transition rate are given in a zip file, available online. GAM, generalized additive model; GLM, generalized linear model.

Parameterization of the MPM and the IPM

To understand the link between phenotypic trait dynamics and population dynamics, we examined the relationship between body size, population density, and each of the demographic and trait-transition rates, using the individual-based experimental data. The demographic rates are the stage-specific daily survival (0 or 1), stage transition (0 or 1), reproduction (0 or 1), and number of eggs conditional on reproduction (≥ 1), whereas the trait-transition rates are the stage-specific daily growth and the average size of eggs produced.

Egg and body sizes were log-transformed for the analyses. The binomial distribution was assumed for modeling survival, transition, and reproduction probabilities; Poisson distribution was assumed for modeling the number of eggs produced minus 1; and Gaussian distribution was assumed for modeling body size growth and egg size. The models were characterized, using generalized linear and additive models (Wood 2006), as the associations between quantitative traits and demographic rates could be nonlinear (Schluter 1988; Kingsolver et al. 2001). We next tested for linear, nonlinear, and two-way interaction effects of body size and weighted population density on each rate. Selection of the most parsimonious model for each of the demographic and trait-transition rates was based on the Akaike Information Criterion (Burnham and Anderson 2002), and the tests for specific effects were based on likelihood ratio tests. The resulting functions were used to parameterize the IPM and the MPM (table 1).

Results

We followed the daily fates of 1,483 eggs, 245 larvae, 275 protonymphs, 275 tritonymphs, 355 adult males, and 355 adult females over the course of the experiment. In addition, 44 eggs were monitored in a separate experiment

for larva-size measurements, as the former experiment did not allow for identifying eggs with larvae. The average body size was 0.18 mm for eggs, 0.24 mm for larvae, 0.35 mm for protonymphs, 0.50 mm for tritonymphs, 0.61 mm for adult males, and 0.73 mm for adult females.

Both the total population size and the abundance at each stage followed a very close trend between the sampling and control populations (fig. 2A, 2B). In response to favorable conditions (i.e., high food and presence of fecund females for 7 days before the start of the analysis), both populations demonstrated a sharp increase in larva numbers during the first couple of days, followed by a sharp decline in larva numbers and an increase in protonymph numbers, eventually settling at a stable trough phase around the thirtieth day. Meanwhile, there were important changes observed in the phenotypic trait distributions. The average body sizes of protonymphs (slope $\pm$ SE, -0.002 ± 0.001 mm per day; $P < .01$), adult males
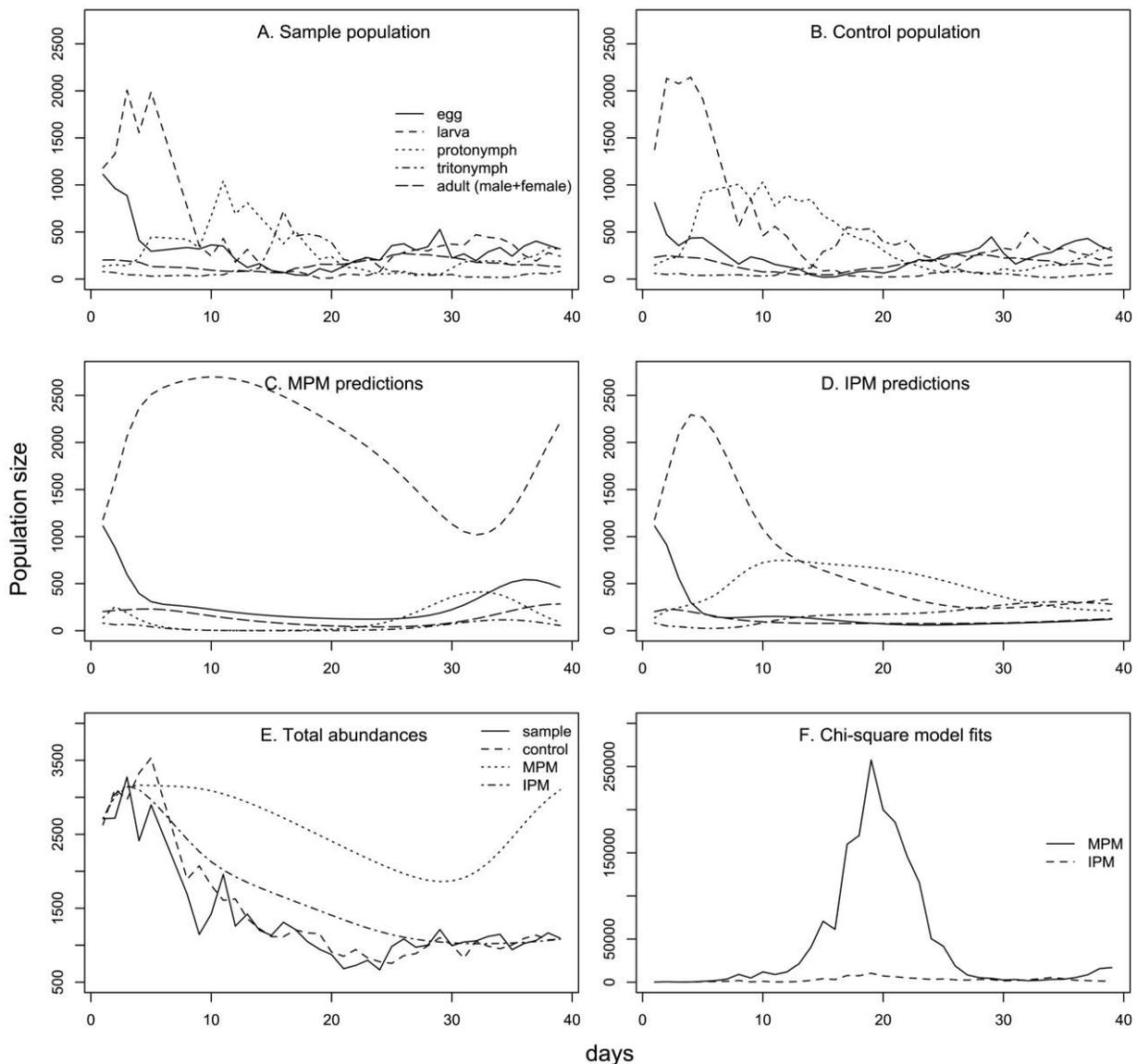

Figure 2: Time series of the abundance in each life-history stage for the sample population (*A*) and the control population (*B*) and as projected by the density-dependent matrix projection model (MPM; *C*) and by the density-dependent integral projection model (IPM; *D*). *E*, Time series of total abundance in the control and sample populations and those projected by the density-dependent MPM and IPM. *F*, Time series of lack of model fit (i.e., total χ^2 values) for the MPM and the IPM.
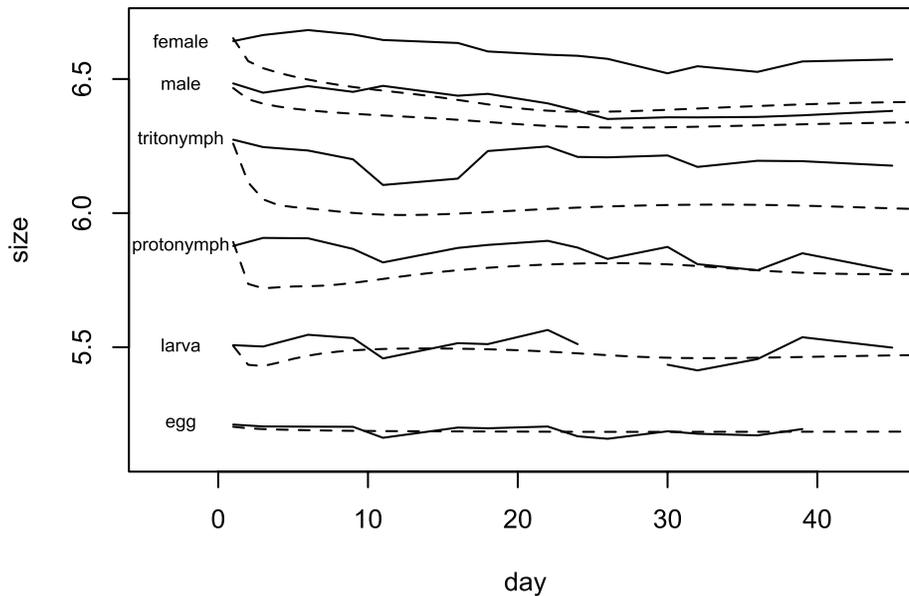
Figure 3: Trends in stage-specific mean body sizes observed in the sampling tube (solid lines) and projected by the density-dependent integral projection model (dashed lines).

(-0.003 ± 0.001 mm; $P < .01$), and adult females (-0.003 ± 0.001 mm; $P < .01$) declined significantly during the transient period (fig. 3).

First we examined the relationship between body size, population density, and each of the stage-specific demographic and trait-transition rates (table 1). Stage-specific survival rates were differentially affected by individual size and population density. In general, smaller eggs had lower survival at low densities (fig. A1*A*; note that figs. A1–A5 are available online in a zip file). Larva and tritonymph survival was affected by population density and body size, which is an integral of past population density; larger individuals had lower survival rates, particularly at lower densities (fig. A1*B*, A1*D*). On the other hand, larger protonymphs had higher mortality at higher densities (fig. A1*C*). Neither body size nor population density had a significant effect on the survival of adult males or females (fig. A1*E*, A1*F*).

Population density and body size also had differential effects on rates of transition to the next stage. In all three intermediate stages, larger individuals had a higher chance of moving to the next life-history stage (fig. A2*B*–A2*D*). Only at very large protonymph sizes did individuals have a lowered probability of maturing into a tritonymph (fig. A2*C*); this is possibly because of larger individuals taking a longer time in the quiescence state. Larger eggs had the highest chance of hatching at lower population densities (fig. A2*A*).

Both the probability of reproduction and the number of eggs produced per day increased with increased maternal size (fig. A3*A*, A3*B*). While the number of eggs increased gradually with an increase in maternal size, an increase in the probability of reproduction was much faster at lower maternal sizes. Both the probability of reproduction and the number of eggs were higher at lower densities, particularly for larger females.

Not surprisingly, larger individuals attained larger sizes the next day (fig. A4). Individuals that made the transition from larva to protonymph and from tritonymph to the adult stages attained larger sizes compared with those that stayed in one stage. In general, increasing population density had a positive effect on the growth of larvae, protonymphs, and tritonymphs. There was also an interaction effect between population density and body size in the protonymph and tritonymph stages; larger individuals grew less at lower densities, whereas smaller individuals grew more (fig. A4*C*, A4*D*).

First we constructed a classical density-dependent, stage-structured matrix projection model (MPM), using the most parsimonious demographic and trait-transition functions that did not include body size as an explanatory variable (fig. A5). The MPM was then used to project the

initial population structure over time. The resulting population projections were able to predict the initial increase in larva numbers but did not capture the subsequent decline (fig. 2C). Overall, the MPM-projected total population sizes were larger than the observed values, mainly because of an overestimation in larva numbers (fig. 2E). The long-term projections (>20 days) showed cyclic dynamics around a stable population size.

Next, using the most parsimonious demographic and trait-transition functions (table 1), we parameterized a density-dependent, size- and stage-structured model (IPM) and projected both the abundance and the mean trait value at each stage over time. The IPM performed substantially better than the MPM in predicting the transient dynamics, capturing the initial increase and subsequent decline in larva numbers and subsequent increase in protonymph numbers (fig. 2D). The differences between the projected and observed population sizes for the IPM during days 10–30 were due to overestimated larva numbers. In general, IPM projections of total population size were closer to the observed patterns than the MPM projections (fig. 2E). A χ^2-based comparison of the model predicted stage structures with those observed in the control population indicated that the IPM performed significantly better than the MPM over a transient phase of 10–30 days; beyond this point, both models had similar performances (fig. 2F). The long-term projections showed cycles with much lower frequency compared with the MPM projections.

The predicted trends in stage-specific mean body size mostly followed the observed trends (fig. 3). Despite the initial mismatch in protonymph and tritonymph body sizes, the projections converged to the observed values after approximately the thirtieth day. There was an underestimation of average body size only in adult females; this was mainly due to the fact that it was not possible to identify the sexes of individuals at the protonymph and tritonymph stages. As a result, in the IPM a tritonymph at a given size was equally likely to become a male or a female, which would not be the case in reality. Nonetheless, body-size projections were able to capture the observed declines in mean body size of both adult stages.

Using a prospective perturbation analysis, we investigated the elasticity of λ (i.e., proportional change in λ) to proportional changes (0.5%) in each of the demographic and trait-transition rates evaluated at different population densities. In general, λ was the most sensitive to changes in the survival and growth rates of four stages (fig. 4). In the MPM analysis, the survival of adult females was the most influential parameter, followed by those of protonymphs and larvae. The λ value was more sensitive to larva survival at low and high densities and to protonymph survival at intermediate densities. The remaining demo-

graphic or trait-transition rates did not have a substantial influence on λ. Although the four most influential stages were the same, the order of stage importance differed between the MPM and IPM analyses. Unlike in the MPM analysis, the tritonymph survival and growth had the largest influence on λ in the IPM analysis, followed by survival and growth in the adult female, protonymph, and larva stages. At very high density levels, survival and growth in protonymphs became significantly more influential, and those in the adult females became significantly less influential.

Discussion

The effect of a change in the biological or physical environment on population dynamics is often mediated through its effects on individuals' physiological conditions and, in turn, vital rates (de Roos et al. 2003). Theoretical and empirical studies have highlighted the role of commonly measured traits such as body size on a population's demographic response to environmental change (Shertzer and Ellner 2002; Reale et al. 2003; Benton et al. 2005; Hairston et al. 2005; Plaistow and Benton 2009; Coulson et al. 2010; Ozgul et al. 2010). In this study, we showed how body size distribution changes over a period of transient response to an experimental perturbation and, in turn, affects several demographic rates. Furthermore, these effects vary among different life-history stages and demographic rates, indicating that either ignoring the mechanistic relationship between individual traits and demography or making coarse generalizations on the causes of individual variability can hinder our understanding of transient population dynamics.

Previous studies on soil mites have investigated the complex interaction between environmental variation, direct and delayed plastic life-history effects (including intergenerational ones transmitted by maternal effects), and population dynamics (Beckerman et al. 2002, 2006; Benton et al. 2002, 2005; Benton and Beckerman 2005; Plaistow and Benton 2009). These studies have shed considerable light on the way in which both density-dependent and density-independent aspects of the environment affect population dynamics (Benton et al. 2006). Despite the accumulated knowledge on these complex interactions, time-series models allowed predictions with only limited accuracy, suggesting that it was necessary to model processes within each stage rather than use simple functions of total density (Benton et al. 2004; Benton and Beckerman 2005). Differences in the demographic performance of different life-history stages create fluctuations in stage structure that are independent of total density and that influence the dynamics. By following the fates and traits of individuals at each stage over different density levels, we provided further
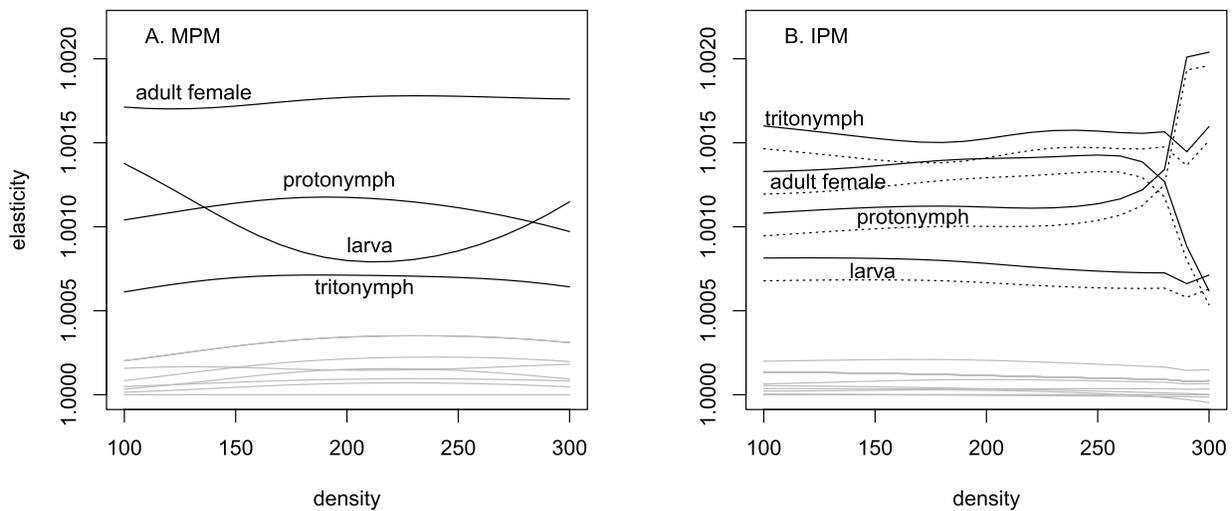
Figure 4: The variation in the elasticity of (i.e., proportional change in) population growth rate to changes in the demographic and transition rates along a population-density gradient predicted by the density-dependent matrix projection model (*A*) and the density-dependent integral projection model (*B*). The solid lines indicate the survival and the dotted lines indicate the growth of larva, protonymph, tritonymph, and adult female stages. All of the other, nonsignificant demographic and trait-transition rates are indicated by solid gray lines.

insight into the mechanisms underlying density dependence in general and how density affects vital rates and body size–demography relationships at each life-history stage in particular.

Our analysis showed that body size had a significant effect on all demographic rates, yet these effects differed among stages. Larger eggs survived better, supporting previous reports on the effect of maternal provisioning on offspring performance (Benton et al. 2005). Previous studies have shown a trade-off between egg size and female fecundity (Benton et al. 2005), but this trade-off was most evident in well-fed females as they aged (and we did not account for maternal age in our current design). Nonetheless, larger females had a higher chance of reproduction and produced more eggs, which accounted for most of the initial population increase. On the other hand, larger individuals at the intermediate stages had higher mortality rates, which is possibly caused by larger individuals having higher metabolic demands that cannot be provisioned at low food availability. In general, well-provisioned individuals had a higher chance of transitioning to the next stage, indicating a developmental threshold on body size (Plaistow et al. 2004).

Our analysis also helped to identify the density effects on stage-specific demographic rates. Both the larva-to-protonymph transition and protonymph survival were inhibited at higher densities, indicating that population declines following the initial high-density phase might be initiated at the protonymph stage. On the other hand, the

low-density environment increased the number of eggs produced, possibly because of lower scramble competition for food among fewer and relatively older females (Plaistow et al. 2007).

Although the density-dependent matrix projection model included the observed density effects on stage-specific demographic rates, it was able to capture the dynamics only during the initial increase phase. MPM projections failed to capture the subsequent decline and the trough phase, suggesting that accounting for density dependence in stage-specific vital rates was necessary but not sufficient (Benton et al. 2004). The integral projection model, on the other hand, included the effects of density and body size–demography relationships and performed substantially better in predicting the transient dynamics compared with MPM. The IPM predictions were able to account for the plastic response in adult body size to changes in food availability and subsequent changes in demographic rates. It is important to note that, although the IPM was able to capture the general population trends better than the MPM, there was still a considerable mismatch in age structure (overestimated larva and protonymph numbers ~15 days after perturbation). An individual-based modeling approach could further improve the predictions of transient dynamics by accounting for previously reported maternal age effects on fecundity and egg size and subsequent maternal effects on offspring life history (Beckerman et al. 2003; Benton et al. 2008). Nonetheless, the relative performance of the IPM compared with that of MPM

highlights the role of the plastic trait response in determining transient population dynamics, and it demonstrates the utility of a trait-based analysis.

Perturbation analysis is a simple first step in answering important questions in evolutionary and population ecology (Caswell 2000) and has proven to be useful in the analysis of stochastic dynamics (Tuljapurkar 1990), and its applications to the analysis of transient dynamics have received wide attention in recent years (Yearsley 2004; Caswell 2007). The proportional change in the population growth rate in response to a proportional change in a vital rate can be used to identify the life-history characteristics that contribute most to fitness (Benton and Grant 1999*a*). However, if density dependence operates at any stage in the life history, ignoring it can result in misleading perturbation results in stochastic environments (Grant and Benton 2000). We used a prospective perturbation of the density-dependent IPM and MPM to identify the most influential rates on population growth. Perturbation of the classical MPM indicated the importance of survival in reproductive female stage and the three intermediate stages leading to it. The perturbation of the IPM provided demographic sensitivities with survival and growth of the same four stages having the highest influence. However, the order of the importance of the four stages differed between the two analyses; the IPM analysis identified the tritonymph stage as the most influential stage. Our previous MPM study also indicated that population growth was more sensitive to adult survival rates than juvenile survival rates (though in that study, juveniles were aggregated into a single stage), but this rank ordering changed as juvenile survival became relatively more important as environmental variation increased (Benton et al. 2004). As in that study, figure 4 indicates that the relative importance of each stage varies with population density and therefore will vary over time in any realistic environment. Furthermore, the differences between IPM and MPM in the relative importance of the four stages indicate that trait dynamics within a stage can have population-level effects, and ignoring these can add further bias to both perturbation analysis results and short-term predictions. These will be particularly important when comparing dynamics and sensitivities between constant (or assumed constant) and stochastic environments.

A major conclusion arising from both theoretical and empirical studies on individual heterogeneity is that the relationship between individual variation and population dynamics is often complex and intertwined. For example, populations with inherently stable dynamics tend to be destabilized by individual variation, whereas those with unstable dynamics can be stabilized (Lindström and Kokko 2002; Filin and Ovadia 2007). These studies highlight the importance of accounting for actual mechanisms

that give rise to individual variation rather than making naïve assumptions on the form of variation (Gonzalez-Suarez et al. 2011). In accordance with these studies, our study shows that an explicit account of mechanisms that give rise to individual variation—trait-demography relationships in general and phenotypic plasticity in particular—improves our understanding of transient responses to environmental perturbations. We demonstrate how a fitness-related individual trait can be plastic enough to respond to environmental perturbations and how the development of this trait can be differentially affected by individual, population-level, and environmental factors. Under these conditions, the resulting heterogeneity among individuals can significantly influence transient population dynamics, and thus ignoring the mechanisms underlying such variation can hinder our population predictions.

In conclusion, we have demonstrated in this model experimental system what we have been observing in several wildlife populations: the intimate link between trait and population dynamics in the face of environmental change. A change in the distribution of a physical trait in response to an environmental perturbation is itself not unexpected. However, our study shows that this dynamic, rather than static, view of individual traits can provide a better understanding of transient population dynamics in the face of environmental change. Ultimately, understanding population dynamics becomes a question of understanding the interaction between the environment and the life history. By considering a relevant focal trait that links environment to individual survival and reproduction, we have provided further insight into the mechanisms underlying a population's numerical and physical responses to a change in the environment.

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