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How well can body size represent effects of the environment on demographic rates? Disentangling correlated explanatory variables

A manuscript in consideration as a standard paper for publication in Journal of Animal Ecology as part of the Special Feature *Demography beyond the Population*

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Summary

1. Demographic rates are shaped by the interaction of past and current environments that individuals in a population experience. Past environments shape individual states via selection and plasticity, and fitness-related traits (e.g., individual size)
are commonly used in demographic analyses to represent the effect of past environments on demographic rates.

2. We quantified how well the size of individuals captures the effects of a population’s past and current environments on demographic rates in a well-studied experimental system of soil mites. We decomposed these interrelated sources of variation with a novel method of multiple regression that is useful for understanding nonlinear relationships between responses and multicollinear explanatory variables. We graphically present the results using area-proportional Venn diagrams. Our novel method was developed by combining existing methods and expanding upon them.

3. We showed that the strength of size as a proxy for the past environment varied widely among vital rates. For instance, in this organism with an income breeding life-history, the environment had more effect on reproduction than individual size, but with substantial overlap indicating that size encompassed some of the effects of the past environment on fecundity.

4. This demonstrates that the strength of size as a proxy for the past environment can vary widely among life-history processes within a species, and this variation should be taken into consideration in trait-based demographic or individual-based approaches that focus on phenotypic traits as state variables. Furthermore, the strength of a proxy will depend on what state variable(s) and what demographic rate is being examined; i.e., different measures of body size (e.g., length, volume, mass, fat stores) will be better or worse proxies for various life-history processes.
Key-words adaptation, demographic rates, environmental effects, multicollinearity, multiple regression, trait-based demography, area-proportional Venn diagram

Introduction

The past and current environments experienced by individuals shape their demographic rates, and these effects can be partially captured in individual state variables such as body condition, mass, and size (Easterling, Ellner & Dixon 2000; Caswell 2001; Benton, Plaistow & Coulson 2006). For many species, size-at-age, body-mass-index, or fat reserves are influenced by food availability and relate to patterns of resource acquisition and storage (Kooijman 2000). Size can be a good proxy for an individual’s general state including developmental stage, resource acquisition and stores, and the outcomes of competitive interactions (Peters 1986). Past experiences shape an individual’s current state, and current state interacts with the current environment to determine the individual fate (i.e., survival, growth, and reproduction). An individual’s full multifaceted state includes its genotype, phenotype, epigenetics, energy reserves and many other variables that can be difficult to measure. Recent research on trait-based demography has highlighted the power of including easy to measure state variables such as individual size in demographic models including matrix and integral projection models (IPMs) (Easterling et al. 2000; Caswell 2001; Ozgul et al. 2009; 2010) and agent-based models (Grimm et al. 2006). However, how much of the past and current environmental effects on demographic rates are captured by individual size and how much variation is left to be explained has not been explored as thoroughly and directly as we aim to here.

The dynamics of state variables and demographic rates are shaped by selection, phenotypic plasticity, and parental effects (Ozgul et al. 2010; Coulson et al.
In many cases, much of the cumulative effects of the past and current environments on demographic rates are integrated into an individual’s size (or condition), but not all (Festa-Bianchet, Gaillard & Jorgenson 1998; Ozgul et al. 2010; DeLong, Hanley & Vasseur 2014). For example, in bighorn sheep, which are considered to be capital breeders, body mass reflects the amount of stored resources available for reproductive effort. Yet, a positive effect of body mass on female reproductive success was only evident at high population densities, a biotic component of the current environment resulting from conditions in the past environment (Festa-Bianchet et al. 1998).

Such cases of weak or context-dependent relationships between an individual’s state and demographic rates can arise from differences in the sensitivity of life-history traits to past and current environments (Le Galliard et al. 2010; Beckerman et al. 2003; Taborsky 2006). Such differences can be due to the fact that selection, plasticity, and parental effects do not affect traits equally (Benton et al. 2006). In addition, context-dependent associations between traits can arise from changes in life-history trade-offs in response to environmental variation that affect patterns of covariation between life-history traits throughout time (e.g., Plaistow et al. 2006; Plaistow and Benton 2009). These examples highlight the complex array of potentially interacting mechanisms shaping life-history and population dynamics and the importance of investigating how much of this variation can be summarized into one easily observable, individual condition-index such as body size (Beckerman et al. 2002; Benton et al. 2006; Evans et al. 2013).
Fig. 1. Influence diagram. Arrows indicate the influence of demographic components on each other. Past environments influence the current environment by shaping the demographic structure and population density. Past environments influence individual states via natural selection, plasticity, and maternal effects. We observe part of an individual’s multifaceted state via its body size. In the soil mite model system, past environments include those an individual has experienced, but also those experienced by maternal, grand maternal and great-grand-maternal generations (Plaistow, Lapsley & Benton 2006).

In this study, we used an extensive laboratory experiment to characterize how demographic rates changed through time in populations experiencing drastically different environments. Our model organism, *Sancassania berlesei* (a soil mite), has a life-history that plastically responds to food availability and population density, and exhibits maternal effects (Benton, Lapsley & Beckerman 2001; Benton, St Clair & Plaistow 2008; Ozgul *et al.* 2012). This experiment enabled us to quantify the influence of individual body size, current environment, and past environment on demographic rates.

Favorable past and current environments lead to better individual states and thus enhanced demographic rates, but a favorable past environment increases population density and can thus reduce the quality of the current environment. The interdependencies of body size, current environment, and past environment (Fig. 1) cause multicollinearity (i.e., correlation) among explanatory variables in regression models that makes it difficult to disentangle the effects (Graham 2003). To disentangle the influence of body size, the current environment, and the past environment, we have used a novel procedure based on the practice of fitting all
possible subsets of these multicollinear explanatory variables (Chevan & Sutherland 1991; Graham 2003; Murtaugh 2009). We modeled potentially nonlinear effects of these explanatory variables on demographic rates using splines (Dahlgren, Garcia & Ehrlén 2011). We teased apart the overlap in explanatory power by comparing the proportion of deviance explained (a generalization of $r^2$, Wood 2006) from models with all subsets of explanatory variables. Overlap in explanatory power is a result of multicollinearity among the explanatory variables, caused by the interdependencies described above. This method is novel because it disentangles multicollinearity in nonlinear splines in a way previously used for linear models (Ip 2001). Also, this paper is the first to plot the results of this decomposition using area-proportional Venn diagrams which are visually intuitive (Micallef & Rodgers 2014). Our goal was to quantify how well the past and current environmental effects on demographic rates were represented by body size, and how much variation was left to be explained.

In the past, researchers have attempted traditional time series decomposition of measured phenotypes in *Sancassania berlesei* and how they change over time (Benton *et al.* 2005) but this is complex because the importance of the past environments vary over time in a way that is itself context dependent (Beckerman *et al.* 2003; Plaistow *et al.* 2006; 2007). So standard linear time series models are not informative. Our new method of decomposing the variability in demographic rates is therefore valuable as it can highlight the importance of processes that we know to be sensitive to conditions in complex ways. Most importantly, it challenges one major assumption underlying recently popular trait-based demographic models: that a focal state variable such as body size captures the effects of past and current environments on the individual’s performance, and acts as a memory mechanism to project the individual performance to future time steps. By using a well-studied system we can benchmark the
performance of the new technique. If the technique produces results that match our
detailed understanding of this model system, we can have confidence that it has utility
for studying systems where the background knowledge is lower.

In the following text, we first describe our methods including the experiment
for our soil mite case study and then statistical analyses including hypothesis testing
and variance decomposition. Then we present results from the case study and divide
our discussion into a soil mite specific discussion and a discussion of the general
applicability of our method for both demographic and general ecological studies.

Materials and methods

Experimental Methods

The goal of our experiment was to observe how population dynamics and
individual demographic rates change in response to vastly different environments that
should induce selection, plasticity, and maternal effects.

Populations of soil mites were raised in 22 mm diameter tubes for nine weeks
in four environments: one constant (control) and three varying (famine, declining, and
fluctuating). Famine and fluctuating populations experienced abrupt changes in their
food (Fig. 2). The experimental timespan is approximately two times the generation
time of soil mites maintained in food conditions similar to our control treatment
(Ozgul et al. 2012; Cameron et al. 2013). Treatments differed in the amount of food
provided and subsequently, population densities naturally varied accordingly (Fig. 2).
All populations experienced a constant food environment prior to the experiment until
population dynamics and stage structure stabilized. The life stages are as follows (in
order): egg, larva, protonymph, tritonymph, and adult (male or female).

There were two replicate sampling populations and five replicate counting
populations per treatment. The counting populations were censused twice per week to
monitor population density and stage structure. There were twenty-eight populations total; more replicates were not possible due to the work required for censusing the counting populations. Twice per week per sampling population, five adult males and five adult females were sampled and placed in five mixed-sex tubes for a period of 24 hours; also three individuals from each juvenile stage (larva, protonymph, tritonymph) were placed in three mixed-stage tubes for a period of 24 hours. Sampling was done several hours after feeding. Sampled individuals were photographed before and after the 24-hour period in which the following responses were monitored: survival (binary), final body length (mm), stage transition (binary), reproduction (binary and egg counts). After the 24-hour monitoring period, surviving individuals were put back in the sampling populations. Eggs were not put back because of the time required to move eggs 0.18 mm in diameter. See appendix S1 for more experimental details.
Fig. 2. Experimental environments and demographic covariates. Each column is a different experimental treatment with two populations per treatment each represented by a line. Each row represents a different covariate: food provided (in mg), naturally varying average individual body size at start of monitoring (length in mm), population density weighted by the average body size in each stage (i.e., total body length per tube), and food supply (food divided by density, i.e., mg food per mm body length). The number of individuals per density unit is equal to the inverse of the stage-specific average length: approximately 4.3 larvae, 3.1 protonymphs, 2.2 tritonymphs, 1.6 males, or 1.4 females, but this varies throughout the experiment as body sizes vary.

Statistical Methods

The goals of our statistical analyses were to determine which demographic responses (i.e., life-history processes) depended on starting body size, current environment, and past environment; then to determine the power of these explanatory variables and how much power overlapped due to multicollinearity.

We quantified evidence of the influence of starting body size, current environment, and past environment on demographic responses using generalized additive mixed models (GAMMs). We used GAMMs because demographic responses potentially have nonlinear dependence on starting body size (Anderson et al. 2008; Dahlgren et al. 2011; Ozgul et al. 2012; Cameron et al. 2013) and we expected responses to change nonlinearly during the experiment in response to the environment. Generalized additive models (GAMs) are convenient because they do not require that one makes assumptions about the shape of the nonlinear relationships. They are generalized linear models that represent the nonlinear relationship using smooth functions of covariates (Wood 2006). GAMMs are GAMs with random
effects in addition to fixed effects, which we use here to account for repeated measures of populations.

Demographic responses of interest were measured after 24 hours for mites sampled from the population (see Experimental Methods). Responses included final body size (length in mm), initiation of transition from one developmental stage to the next (binary), reproduction by females (binary), fecundity (number of eggs laid given reproduction), egg size (in mm, average within female), and survival. In trait-based demography, it is common to model the growth process as an individual’s size at the end of a time step dependent on its size at the start of the time step, so we follow that standard and use “final body size” and “growth” interchangeably.

Explanatory variables of interest included starting life-history stage (the stage of an individual at the start of a 24-hour monitoring period), starting body size, current environment, and past environment; see the following three paragraphs for further descriptions of starting body size, current environment, and past environment (Fig. 1). For clarity, we consistently refer to these four components as “explanatory variables”. Alternatively, we use “covariates” to refer to the observed variables included in the smooth functions that make up these explanatory variables.

The explanatory variable “body size” (i.e., starting body size) was a smooth function of an individual’s observed body size at the start of the 24-hour monitoring period. Throughout this text, all discussions of the explanatory power of body size are referring to this starting body size explanatory variable.

The explanatory variable “current environment” was a two-dimensional smooth function of the most recent estimate of (i.e., within the past 24 hours) population density and food supply (used here to mean food given divided by density; density and food supply are further described below). Two-dimensional smooth
functions allow for nonlinear effects of the covariates and their interaction. The fit of a two-dimensional smooth function results in a three-dimensional nonlinear surface, the height (i.e., third dimension) of which represents how the response variable changes with the covariates. We assumed that the current environment experienced by an individual is an interaction between the population density and the available food. Population density (per tube) was calculated as the number of individuals in a given stage times the average body size in that stage, summed across all stages, except eggs, to account for asymmetric competition. See appendix S2 for details of our density calculations. Food supply (food given divided by density, i.e., mg food per mm body length) was used as a covariate (as part of the current environment smooth function) instead of absolute food because preliminary analyses indicated that it was a better predictor of all demographic responses.

The explanatory variable “past environment” was a treatment intercept and a smooth function of the day of each treatment. When specifying a smooth function of a continuous variable by a categorical variable in a GAM (as in our past environment by treatment), it is usually necessary to include a separate intercept for that categorical variable. Our treatment intercepts are parameterized in the standard way with the control treatment as a baseline and other treatments as contrasts. The smooth functions of time are not tied to any informative covariates and can take any nonlinear shapes that are smooth through time and thus account for cumulative changes in demographic responses that arise through selection, plasticity, or parental effects. This flexibility can incorporate the cumulative effects of the environment up to the moment a demographic response is observed which encompasses much of what we call the “current environment” i.e., the most recently estimated population density and food supply. Thus, effects of the environment before this “current environment” should be
evident in explanatory power from the “past environment” that does not overlap that of the “current environment”. The “past environment” spline was defined in such a flexible way so that, in a full model with all explanatory variables, it can pick up any population level patterns not explained by individual body size, population density, or food supply. This implies that, given two individuals of the same body size in the same current environment in different treatments or different times in the same treatment, we assume that any differences in their demographic rates are caused by differences in their past environments. It is possible that there are aspects of the current environment that differ, but are not incorporated into our current environment spline. So this interpretation of the residual patterns is not strong evidence but a means of generating hypotheses that could be tested with further experiments that are more mechanistic.

For example, the full GAMM fit to egg counts (fecundity) contained a smooth function of starting body size, a treatment intercept, a smooth function of the day for each treatment, a two-dimensional smooth function of the population density and food supply, and a random effect of population. The hypothesis represented by this model is that an individual’s fecundity depends on its current access to food and the body size of that focal individual (which determines its competitive ability). However, the allocation strategy of individuals in some treatments or time points of treatments may differ from individuals of similar size in similar current environments due to differing past environmental experiences. These differences due to past environmental experiences should appear in the non-overlapping explanatory power of the past environment spline.

To be clear, as part of the GAM fitting procedure, the smooth functions described above took on different nonlinear shapes (thin-plate regression splines) for
each model just as coefficients would differ among linear models. Variation in a
demographic response can be explained by one explanatory variable in one model and
a different explanatory variable in a different model that contains a different set of
variables. This is the same issue that occurs when estimating coefficients in linear
multiple regression with correlated explanatory variables (Chevan & Sutherland 1991;
Graham 2003). Multicollinearity hinders the interpretability of the coefficients and
smooth functions (Mitchell-Olds & Shaw 1987).

For each demographic response separately, we fit the full GAMM containing
all explanatory variables described above. We applied Wald-type tests to the full
GAMM (Wood 2013b); these are p-values indicating the strength of evidence against
the null hypothesis that explanatory variables have no influence. We also examined all
submodels of the full GAMM using information theory and results were similar to the
Wald-type tests; the details including R code can be found in appendix S3.

For demographic responses whose supported explanatory variables contained
starting body size, current environment, or past environment we calculated the
explanatory power of each of these and their overlap. We focused on these
explanatory variables because they were relevant to all responses whereas life-history
stage only applies to some responses and may not apply to all species. Unlike models
that tested for effects, to simplify the interpretation of explanatory power, these
contained no random effect. It is possible to expand this method to apply to mixed
models, but this is beyond the scope of this paper (Nakagawa & Schielzeth 2012).

We fit GAMs with all subsets of the supported explanatory variables. We calculated
the overlap in explanatory power as the difference from what the explanatory power
of a model with multiple variables would be if it were additive relative to single
variable models. The non-overlapping explanatory power is the increase in
explanatory power when adding a variable to a model that already contains other variables. These calculations have been previously described for variance partitioning in linear models (Chevan & Sutherland 1991; Ip 2001; Grömping 2007).

Other statistical methods exist for dealing with multicollinearity, but they do not address our interest in interpreting both the overlapping and non-overlapping portions of explanatory power to get insight into the demographic processes that lead to multicollinearity (Graham 2003). Principal components analysis takes many predictors and summarizes them into just a few, but we wanted to look at all of the predictors and their relationship with body size. Residual and sequential regression require that you assume some hierarchy among the explanatory variables, but we wanted to see if body size was more important, not assume it. Structural equation modeling and path analysis can not handle relationships as flexibly as GAMs and we wanted our method to be able to pick up minor nonlinearities in the time series (Brandt, Kelava & Klein 2014). For these reasons, we have expanded upon existing methods and combined existing tools in new ways to produce a new method for examining multicollinear predictors that have nonlinear relationships with the response variable.

All GAMMs were fit in R using gamm4 with lme4 and GAMs were fit using mgcv (Wood 2013a; Bates et al. 2013; Wood & Scheipl 2013). For smooth functions, we used penalized thin-plate regression splines that tend to give the best mean squared error (Wood 2003; 2013a). All continuous covariates except day were standardized to have mean zero and unit variance. We allowed smooth functions of starting body size, current environment, and past environment to have a maximum of five, ten, and ten knots respectively. Five knots for the effect of starting body size were previously discussed by (Dahlgren et al. 2011). Because current environment was a two-
dimensional spline, we assumed it might need more knots. Examination of the responses (Fig. 3) suggested that they might be more flexible through time (i.e., past environment). The mgcv package automatically reduces the flexibility of splines based on maximum likelihood using the Laplace approximation. All models used typical distributions and link functions for the responses as follows: final body size was Gaussian (identity link); stage transition was binomial (logit link); reproduction was binomial (logit link); non-zero fecundity minus one was Poisson (log link); survival was binomial (logit link).

**Results**

In each experimental environment, demographic responses varied through time and with some consistency between the two replicate populations (Fig. 3). Wald-type tests applied to the full model indicated that starting body size and the current environment had effects on most demographic rates (Table 1). Development and reproductive rates were higher for individuals with larger body sizes and in environments with higher food supply (appendix S5). Higher density decreased growth and reproductive rates, but had a positive effect on transition probability with marginal significance (Table 1 and appendix S5). While controlling for the effects of body size and the current environment, declining and fluctuating environments also caused temporal patterns for some demographic rates (Table 1 and appendix S5).
Fig. 3. Observed life-history processes.

Each column represents an experimental treatment. Each row represents a life-history process observed over a 24 hour monitoring period: final body size at the end of monitoring (length in mm), probability of initiating transition from one developmental stage to the next, probability of reproduction (given female), fecundity (number of eggs laid given reproduction), egg size (in mm, average within female), and survival. Lines represent the mean of individuals sampled from a population on a given day (a subset of the population: 5 from each adult stage and 3 from each juvenile stage). Grey ribbons represent +/- 2 standard errors. Standard errors are missing for egg size.
on days when only one female was sampled. Observations in the famine populations
ended when all individuals died. The control populations persisted to the end, but
observations ended. ‘Proto’ refers to protonymph and ‘trito’ to tritonymph.
Table 1: Wald-type tests (to test the null hypothesis that the smooth function was not different from 0) applied to all smooth functions in the full GAMMs. The control intercept was used as the baseline for treatment contrasts and was always non-zero (**). The growth model containing stage gave a convergence warning, so we omitted it (see appendix S3 for details). ‘NA’ indicates that stage was not included in a model to distinguish this case from non-significance. ‘Proto’ refers to protonymph and ‘trito’ to tritonymph.

‘.’ p<0.1, ‘*’ p<0.05, ‘**’ p<0.01, ‘***’ p<0.001

<table>
<thead>
<tr>
<th>Stage</th>
<th>Body size</th>
<th>Current environment</th>
<th>Past environment smooth functions (and intercept in parentheses)</th>
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<tbody>
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<td></td>
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<td>Control</td>
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<tr>
<td>Growth</td>
<td>NA</td>
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<td>***</td>
</tr>
<tr>
<td>Transition</td>
<td>***(proto)</td>
<td>***</td>
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<tr>
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<td>***(trito)</td>
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</tr>
<tr>
<td>Reproduction</td>
<td>NA</td>
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<tr>
<td>Fecundity</td>
<td>NA</td>
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<tr>
<td>Egg Size</td>
<td>NA</td>
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<tr>
<td>Survival</td>
<td>*(trito)</td>
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Power of supported explanatory variables

The best explanatory variable of growth and stage transition was body size (Fig. 4).
Both reproductive rates depended more on the environment than on female body size (Fig. 3). Body size encompassed almost all of the explanatory power of the current and past environments for growth (0.99); 0.27 and 0.26 respectively for stage transition; 0.39 and 0.34 respectively for reproduction; and 0.47 and .48 for fecundity (numbers are proportion of explanatory power overlapping). See Appendix S4 for explanatory power calculations. As is common for variance decompositions, some shares came out slightly negative so we rounded these to zero for graphing in Fig. 4 (Hamilton 1987; Ip 2001); these were an order of magnitude smaller than the portions we interpret (Growth: se=-0.001; Transition: se=-0.007, sh=-0.005). This indicates that one variable was masking a tiny amount of the explanatory power of another variable (Hamilton 1987). This omission is why the subareas do not perfectly add up.
Fig. 4. Overlapping explanatory power of starting body size (s), current environment (e), and past environment (h). Each panel contains an area-proportional Venn diagram (Micallef & Rodgers 2014) of explanatory power for a demographic response: final body size after 24 hours (Growth), probability of initiating stage transition (Transition), probability of reproducing (Reproduction), and Fecundity. Areas of the ellipses within a panel represent the proportion of null deviance explained by models with one of the explanatory variables. Subareas, designated with letters and quantities, represent explanatory power attributable to one, two, or three of the explanatory variables due to interdependence of the variables. Labels of zero areas were omitted. The total explanatory power of a component is the sum of the subareas, noted at the top of each panel. See Appendix S4 for calculations.
Discussion

Predicting life-history and population responses to changing environments has long been the focus of population ecologists (e.g., Williams 1966). Trait-based demographic models have highlighted the strength of including state variables such as body size to understand and predict population dynamics (Easterling et al. 2000; Caswell 2001; Ozgul et al. 2010). However, these models rely on the assumption that chosen state variables are a good proxy of the effects of the environment on demographic rates. Here, we challenged this assumption by investigating how well body size represented the integrated effects of environmental sequences by quantifying the dependence of demographic responses on individual body size, current environment, and past environment in a well-studied soil mite experimental system. To do so, we used a quantitative method for decomposing the effects of multicollinear explanatory variables, extended to allow for nonlinear relationships and graphically presented using area-proportional Venn diagrams.

The past environment explanatory variable was designed to pick up population level patterns after controlling for the effects of body size and the current environment. This should include delayed effects from past environments experienced by individuals and their mothers. Although not all of these splines were significantly different from zero, examining the patterns is useful for generating hypotheses to be investigated with more detailed data and more mechanistic models. Here, we demonstrate this with the soil mite model system because many mechanisms are already known.

We found that the total explanatory power of body size and the amount of environmental effects encompassed by body size strongly varies among demographic responses. Although this general result is already known, we demonstrate that the
strength of our method lies in its flexibility, making it easily applicable to data limited
situations, which are common in ecology. It is a useful tool to identify patterns and
test for the ability of state variables to encompass environmental effects on
demographic and life-history responses that can later be explored with more
mechanistic experiments.

The case of soil mite populations in drastically different environments

Developmental rates depended more on body size than past or current
environments, and reproductive rates were more strongly affected by the
environments than by body size. For final body size (i.e., growth), the effect of the
environment was almost fully encompassed by starting body size, while for other
demographic responses, body size only accounted for a quarter to half of the
environmental explanatory power. These results demonstrate that demographic
responses differed in their sensitivity to the environment and the proportion of
environmental effects transmitted through an individual’s body size (e.g., Ozgul et al.
2012; Ozgul et al. 2010).

We expected to find significant effects of the past environment on
developmental rates because previous work demonstrated that soil mites can exhibit
strong delayed life-history effects in response to densities and food regimes
(Beckerman et al. 2003; Plaistow et al. 2006; Cameron et al. 2013). However, in our
experiment, these effects were almost completely overlapped by the current
environment. Previous experiments, that found effects of past environments on
development rates utilized very different food levels (high vs low food for individuals,
or stochastically varying food with high frequency for populations) (Beckerman et al.
2003; Plaistow et al. 2006; Cameron et al. 2013). In the current experiment, on a daily
basis, food and population density was strongly autocorrelated, meaning that current
and previous environments were on average similar across the experiments. Under
these conditions, the impact of current conditions on developmental rates was very
strong. One exception was in the fluctuating environment where, after controlling for
the effects of body size and the current environment, developmental rates declined
over time (supplementary Fig. S1). This could be due to delayed density dependence
driven by the high densities during the first 3 weeks of the experiments in response to
the first peak of food availability (Beckerman et al 2003, Benton et al 2005). Cohorts
of juveniles born under high densities grow and develop slowly and can only recruit
when competition for food is very low (Benton et al 2005). In the fluctuating
treatment, competition for food was very low at the beginning of the second peak of
food availability, when density was low, leading to a peak of fecundity and generating
a new cohort of juveniles born under even higher densities.

As expected, our results indicate that females adjusted their reproductive effort
according to their environment more than their current body condition (Fig. 4). Reproduction increased with food availability, which was especially evident in the
fluctuating environment where a ten-fold rise in reproduction coincided with a spike
in food supply (Figs 2 and 3). For both reproductive rates, the explanatory power of
the environment not encompassed by body size was substantial (Fig. 4). Under these
experimental conditions, female soil mites were on the income breeding end of the
income to capital breeding life-history continuum, relying more on current income
than on stored resources for reproduction (Stearns 1989). However, we know that
under conditions where food differs radically between different parts of the life-
history, females raised in low food environments are lower quality and when given
excess food as adults are much less fecund than females raised in high food
environments (Beckerman, Benton et al. 2003). It is possible that the duration of our fluctuating food experiment was not long enough to observe the effects of this. We hypothesized in Fig. 1 that the past environment can affect demography via the individual's state. We can observe this as an overlap between the explanatory power of body size and the past environment. Interestingly, fecundity showed substantial overlap between these two components. So a portion of the effects of the past environment experienced by a female and her ancestors (effects we know exist in this model organism) were integrated into body size.

After accounting for the effects of body size and current environment, the gradually declining environment further reduced both reproductive rates. Also, the past environment had 6% non-overlapping explanatory power. Together, these results support previous findings that females adjust their reproduction through a combination of evolutionary, plastic, and maternal effects in addition to their current environment and condition (e.g., Plaistow et al. 2007; Benton and Plaistow 2008, Cameron et al 2013).

**Unexplained demographic rates in the soil mite case study**

Observed daily survival of individuals was independent of environments and body size and may have been artificially high due to reduced density dependent effects during the 24h of sampling. Maternal effects on egg size were not observed in this experiment, but effects may have been transmitted through unobserved pathways such as epigenetics (Youngson & Whitelaw 2008) or nutrient investment (Benton et al. 2008). Transition rates only responded to the environment with marginal significance. Although our experimental design did not allow for collection of further data, the estimation of some of the vital rates can be improved by increasing the sample sizes in future experiments (Fig. 3).
General applicability

The soil mite *S. berlesei* is an attractive model system because much is known about the potential interplay between current and past environments in determining phenotypic variation (Beckerman *et al.* 2003; Plaistow *et al.* 2006; 2007); yet a critical conclusion from the detailed work on individuals under controlled conditions is that the interaction between current and past environments to determine the phenotype is itself highly plastic. The purpose of this investigation was not to develop a mechanistic understanding of an already well-studied system. Instead, this new variance decomposition method is useful because it is a way of generating an overall picture across a range of environments, of the average interplay between historical and current drivers of phenotypic dynamics.

More generally, this method is useful for examining the shared and unique contributions in multiple regression beyond demographic studies, including linear and generalized linear regression. Researchers often wonder which explanatory variables have the greatest influence on their responses – a complicated issue when there is multicollinearity among explanatory variables (Graham 2003). The method described by Ip (2001) and used here for intuitively visualizing the shared explanatory power and interdependence of variables has not yet been adopted by the ecological literature. Here we have expanded upon this method by applying it to nonlinear regression using GAMs rather than linear regression and presenting the results using area-proportional Venn diagrams (Micallef & Rodgers 2014). We propose this method as a technique complementary to those discussed by Graham (2003), including principal components regression, structural equation modeling, and residual and sequential regression.
Future work could extend this method further to include confidence intervals estimated by bootstrapping.

In demographic studies, there are more mechanistic ways of quantifying the effects of the environment and individual states on life-history processes and population dynamics than our method. More mechanistic methods will lead to stronger inference and the ability to make predictions. These include physiologically structured population models which characterize individuals based on multiple physiological traits such as their size, age, stage, and energy reserves (de Roos 1997). They also include mechanisms such as the consumption and digestion of resources. These models require either data detailed enough to parameterize or a priori assumptions about the underlying physiological mechanisms. As is the case in most experimental and wildlife population studies, we did not have such detailed data available in this study. However, our non-mechanistic model has the strength of being flexible enough to apply in these data-limited situations and will be useful for identifying patterns and generating hypotheses that can later be explored with more mechanistic models and experiments with more detailed data collection.

The demographic method presented here can be applied to any dataset in which an individual state variable, individual fates, and relevant environmental covariates are available for a population in a variable environment, including data from wild plant and animal populations e.g., St John’s wort (Buckley, Briese & Rees 2003); Soay sheep (Ozgul et al. 2009); yellow-bellied marmots (Ozgul et al. 2010). When sufficient data are available to develop mechanistic demographic models, the assumption that the state variables chosen are good proxies of the environmental effects on phenotypic traits should be tested. If, as in our study, the state variables only encompass a small portion of the effect of the environment, then additional
environmental variables may need to be measured and included as predictors. Several IPMs (e.g. Ozgul et al 2012, Coulson 2011) and physiologically structured population models (e.g., Persson & de Roos 2006; Le Bourlot, Tully & Claessen 2014) accounted for current environmental effects on life history and demography. Also these types of models can implicitly account for delayed life-history effects because the past environment can affect the current state of individuals and thus their life-history trajectory (de Roos et al. 2003). However, an explicit consideration of the past environment on demographic responses is so far missing, mainly due to the difficulty of mechanistically modeling delayed life-history effects such as delayed density dependence (Beckerman et al. 2003), and this is one of the main challenges left to be achieved to improve the predictions of mechanistic demographic models.

Overall, body size and environmental variation are simply variables that were convenient for answering the bigger question of how good is an easily observable, individual state variable as a proxy for the nutritional effects of environments in a population model. A comparative study using the approach presented here could offer further refinement of our understanding of what kinds of organisms (e.g., capital vs. income breeders) and patterns of environmental variations (e.g., magnitude and temporal frequency of variation relative to generation time) are most likely to be associated with a complex and limited ability of a single individual state variable to predict demographic rates.

Data Accessibility

Data is available from Dryad Digital Repository:

http://dx.doi.org/10.5061/dryad.pq161

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Supporting Information

The following Supporting Information is available for this article online

Appendix S1: Details of Lab Experiments

Appendix S2: Density Calculations

Appendix S3: Model Selection and Full GAMM (R Code with Output)

Appendix S4: Decomposing Explanatory Power and Drawing Euler Diagrams (R Code with Output)

Appendix S5: Full GAM Fits and Splines (R Code with Output)

Figure S1: Effects of Past Environment

References


