Context-Dependent Intergenerational Effects: The Interaction between Past and Present Environments and Its Effect on Population Dynamics

Stewart J. Plaistow,[1,*] Craig T. Lapsley,[2,†] and Tim G. Benton[3,‡]

1. School of Biological Sciences, Zoology Building, University of Aberdeen, Aberdeen AB24 2TZ, United Kingdom;
2. Wellcome Centre for Molecular Parasitology, University of Glasgow, Glasgow G11 6NU, United Kingdom;
3. School of Biology, University of Leeds, Leeds LS2 9JT, United Kingdom

Submitted May 10, 2005; Accepted September 7, 2005; Electronically published December 12, 2005

ABSTRACT: Intergenerational effects arise when parents' actions influence the reproduction and survival of their offspring and possibly later descendants. Models suggest that intergenerational effects have important implications for both population dynamical patterns and the evolution of life-history traits. However, these will depend on the nature and duration of intergenerational effects. Here we show that manipulating parental food environments of soil mites produced intergenerational effects that were still detectable in the life histories of descendents three generations later. Intergenerational effects varied in different environments and from one generation to the next. In low-food environments, variation in egg size altered a trade-off between age and size at maturity and had little effect on the size of eggs produced in subsequent generations. Consequently, intergenerational effects decreased over time. In contrast, in high-food environments, variation in egg size predominantly influenced a trade-off between fecundity and adult survival and generated increasing variation in egg size. As a result, the persistence and significance of intergenerational effects varied between high- and low-food environments. Context-dependent intergenerational effects can therefore have complex but important effects on population dynamics.

Keywords: life-history plasticity, context dependence, intergenerational effects, *Sancassania berlesei*, population dynamics.

* Corresponding author. Present address: Department of Animal and Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, United Kingdom; e-mail: s.plaistow@sheffield.ac.uk.

† E-mail: ctl2x@udcf.gla.ac.uk.

‡ E-mail: t.g.benton@leeds.ac.uk.

Am. Nat. 2006. Vol. 167, pp. 206–215.

Intergenerational effects arise when an individual's actions affect not only its own survivorship and reproductive performance but also those of its offspring and potentially those of later descendants (Andersson 1978; Livnat et al. 2005). From a population dynamic perspective, these effects are important because they mean that a population's response to environmental change may be time-lagged to some degree, with intergenerational effects operating as a source of intrinsic delayed density dependence (Rossiter 1994; Beckerman et al. 2002). It is well known that delayed density dependence can destabilize population dynamics and promote cyclic dynamics (Turchin 1990; Royama 1992). For this reason, intergenerational effects have been put forward as potentially important determinants of long-term population dynamic patterns (Ginzburg and Taneyhill 1994; Bjørnstad et al. 1998; Ginzburg 1998; Inchausti and Ginzburg 1998; Benton et al. 2001*a*; Coulson et al. 2001; Dennis et al. 2001; Beckerman et al. 2002; Lindstrom and Kokko 2002; Kendall et al. 2005). However, the nature and magnitude of intergenerational effects on population dynamics is still a topic of much debate (Benton et al. 2001*a*, 2005; Ergon et al. 2001*a*; Turchin and Hanski 2001; Lindstrom and Kokko 2002; Oksanen et al. 2002). The effect observed in a model may be critically dependent on the details of the model, including the traits that are affected (Bjørnstad and Hansen 1994; Benton et al. 2001*a*; Lindstrom and Kokko 2002).

Currently, population models have really considered only single-generation intergenerational effects (i.e., maternal effects) that are modeled as a positive association between the quality of the mother and the quality of the offspring that is expressed as an increased rate of reproduction (Ginzburg and Taneyhill 1994; Ginzburg 1998; Inchausti and Ginzburg 1998; Benton et al. 2001*a*). This assumption is simplistic for at least three reasons. First, mothers in good condition may sometimes have a negative effect on the fitness of their offspring (Bernardo 1996*b*;

Einum and Fleming 2000; Benton et al. 2005). Second, intergenerational effects may interact and influence the expression of life-history traits in complex ways (Bernardo 1996*a*; Fox and Savalli 1998; Hercus and Hoffman 2000; Magiafoglou and Hoffmann 2003). Finally, intergenerational effects can be context dependent, affecting traits differently in different environments (Berven 1990; Gliwicz and Guisande 1992; Parichy and Kaplan 1992; Bernardo 1996*b*; Czesak and Fox 2003; Lardies et al. 2004; Räsänen et al. 2005; Stillwell and Fox 2005). Immediate environmental conditions may even completely override intergenerational effects (Weiner et al. 1997; Ergon et al. 2001*a*). Accordingly, the incorporation of intergenerational effects into population dynamic models requires an understanding of how intergenerational effects influence the whole life history of organisms in different environments over multiple generations.

Extracting detailed information on the strength and duration of maternal effects from field data is fraught with difficulty, as one has to disentangle the effects of changes in juvenile density from changes in juvenile quality and from cohort effects created by other aspects of the immediate neonatal environment (Albon et al. 1987; Lindstrom 1999; Metcalfe and Monaghan 2001). We therefore undertook an experimental study to measure the strength of intergenerational effects on a number of life-history traits in a number of different environments over three generations, using the soil mite *Sancassania berlesei*. The experimental design was a crossed factorial design, where the first factor was the food in the parental (P) generation and the second factor was food in the filial generations (i.e., the F_1, F_2, and F_3 generations). This design enabled us to separate out the relative influence of current and past environments on multiple key life-history traits and measure the nature, strength, and duration of intergenerational effects across a range of environmental backgrounds.

Material and Methods

Study Organism

The *Sancassania berlesei* used in these experiments were taken from a laboratory culture that was originally collected from an agricultural manure heap in 1998. The stock was fed a level half-teaspoonful of yeast granules per day since being taken from the wild. This level of feeding translates as a "low" per capita food quantity, as evidenced by the small size of adults when they are taken directly from the stock culture. The consistent size of the animals removed from stock suggests that the population had reached an equilibrium size. Details regarding basic experimental techniques and information about the basic biology of *S. berlesei* can be found elsewhere (Benton et al. 2001*b*).

Experimental Design

Replicated common-garden cultures were initially set up from the stock cultures. These cultures were kept in tubes as described by Benton et al. (2001*b*). Each tube was supplied with food ad lib. in order to maximize egg production. Six hundred eighty eggs from second-generation females were collected from a single 24-h laying period and then randomly sorted into batches of 20 and reared in 34 identical culture tubes (Benton et al. 2001*b*). All the tubes were fed and watered once a day. Food consisted of a "hole punch" disk of filter paper (diameter 6 mm) onto which a drop of yeast solution had been dropped and left to dry in an oven. We used 0.5, 0.06, and 0.02 g 10 mL^{-1} yeast solutions as high-, medium-, and low-food treatments, respectively. In this experiment, the high-food treatment provided sufficient food for juveniles to grow at a maximum rate and mature at sizes close to maximum. Comparison of the results here with those of other experiments indicates, however, that high food is insufficient to produce maximal adult performance (e.g., fecundity), so the terms high, medium, and low food are relative rather than absolute. Six of the 34 tubes were fed high food, six were fed medium food, and 22 were fed low food. All of the tubes making up the parental generation were checked once a day, and upon maturation tubes were set up, each with 10 pairs of adults from the same feeding regime. Eggs laid 4–6 days after the adults were paired were then used to set up the F_1 generation. Replicated batches of 20 F_1 eggs from each parental feeding treatment (high, medium, and low) were then reared in one of three offspring feeding regimes (high, medium, and low), resulting in nine F_1 treatment combinations (HH, HM, HL, MH, MM, ML, LH, LM, LL). Data were collected from three replicate tubes in each treatment group. Individuals maturing from surplus replicate tubes within each treatment were used as backups to ensure that we had sufficient numbers to set up subsequent generations. The experiment was continued for a further two generations on the offspring feeding regimes, with each replicate of each treatment in each new generation being set up with 20 eggs laid on days 4–6 by individuals within the same treatment group but from the previous generation (see fig. 1).

Measuring Juvenile Life-History Traits. After the new tubes were set up in each generation, the eggs in the three data replicates for each treatment group were photographed using a Canon Powershot S40 digital camera connected to a Vision Engineering Lynx stereo microscope at × 40 magnification. Eggs were then measured from tip to tip

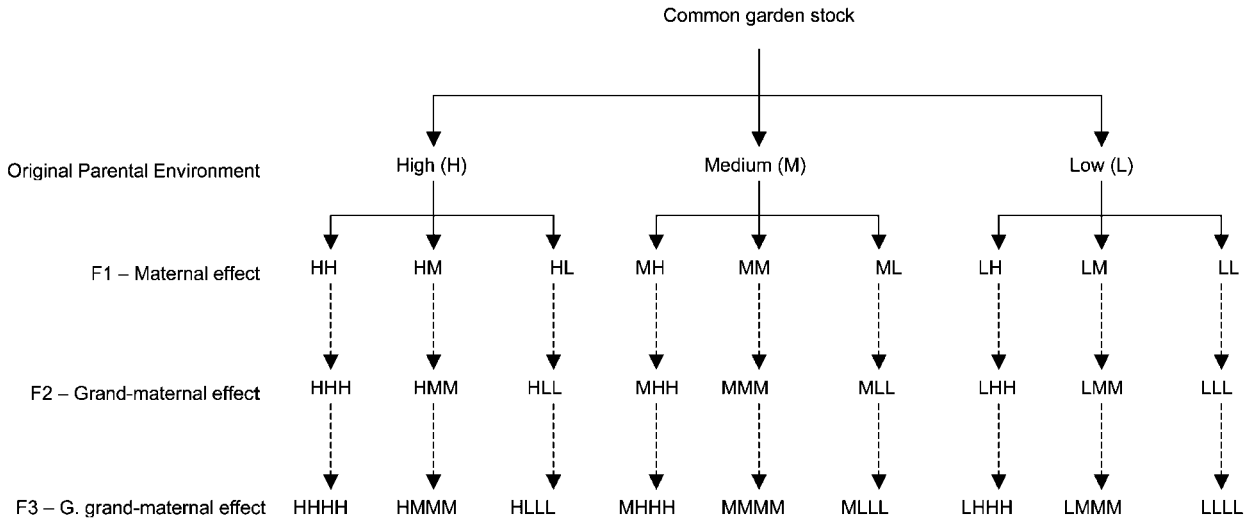


Figure 1: Schematic illustrating the design of the experiment. By manipulation of food conditions in the original parental environment, three different types of mothers were created. Eggs from these mothers were then reared in either high-, medium-, or low-food environments for a further three generations, enabling us to track the significance and persistence of the initial perturbations on the life-history strategies of subsequent descendants (see "Material and Methods" for a detailed explanation).

using the ImageJ 1.28u image analysis package (http://rsb.info.nih.gov/ij) and were used to calculate a mean egg size for each treatment tube. We recorded the sex and age at maturity (to the nearest day) of all individuals maturing from three replicates within each of the treatment groups. Newly matured animals were then photographed as for eggs. Length was measured as the distance from the tip of the hypostome to the tip of the opisothoma using the ImageJ 1.28u image analysis package. Recruitment was measured as the number that survived to maturity out of the initial 20 eggs.

Adult Life-History Traits. From the adult tubes, we recorded the number of males and females surviving in each tube every day. To avoid density-dependent effects, dead animals were replaced with males from backup tubes. The female survival data were used to generate survival curves and the average estimated survival probability of females in each tube with the *survreg* function in R (Ihaka and Gentleman 1996; Harrell 2000). On every third day, we transferred all of the adults to a fresh tube, except on days 4, 5, and 6, when adults were transferred to a new tube each day and the eggs laid were counted. The mean per capita fecundity per tube was calculated for days 4–6 by averaging the daily number of eggs laid and dividing it by the number of females present.

Statistical Analysis. We used MANOVA to examine how original parental environment (high, medium, low), current food environment (H, M, L), and time (generation F_1, F_2, or F_3) influenced the mean size of egg individuals hatched from, mean age at maturity, mean size at maturity, mean juvenile recruitment, mean survival, and mean fecundity (measured over days 4–6). General linear models with each of the above variables as the response variable and original parental environment, generation, and current food environment as categorical explanatory variables were then used to further investigate the MANOVA results and to establish the relative sensitivity of the different traits to past and present environments. In all analyses, we fitted full models to the data and then used a backward-stepwise procedure to remove interactions that had no significant effect. We used R^2 values to assess the proportion of variance in each trait that was explained by each term in the model. Separate factor analyses were carried out for each current food environment (H, M, L) in order to examine how covariation between different life-history traits—including variation in egg size (the source of all intergenerational effects)—changed in different environments. The number of factors extracted using the principal components method was determined by including components that had an eigenvalue >1, and a varimax rotation was used to obtain clear loading patterns and simplify interpretation of the results (StatSoft 2004). Because all treatments were set up with 20 eggs in each generation, any observed intergenerational effects must have derived from variation in egg quality rather than variation in egg number. Consequently, in order to examine how egg size varied

in different food environments over the course of the experiment, we carried out a further general linear model with grandmaternal food environment and maternal food environment each fitted as a separate three-level fixed factor (H, M, L).

Results

Do Past Environmental Conditions Have Any Effect on Life-History Variation?

MANOVA indicates that variation among the life-history traits measured in this experiment (recruitment, egg size, age at maturity, size at maturity, fecundity, survival) was significantly related to the mites' current environment and the original environment in the parental generation. The significant interaction between original parental environment, current environment, and generation suggests that the effects of an interaction between original parental environment and current environment varied from generation to generation (table 1; fig. 2). The results were similar when only F_1 and F_2 generations were considered or when all three generations were considered with medium and low current food treatments combined. Figure 3 shows that there were still effects of the original parental background in the F_3 generation, but these were not apparent in all traits in all current food environments.

Table 1: Effect of current food environment, original parental environment, and generation on life-history trait variation

Source	df	Wilks's λ	*F*	*P*
MANOVA 1:				
CFE	6, 35	.066	82.742	<.001
P	12, 70	.345	4.098	<.001
G	12, 70	.248	5.872	<.001
CFE × P	12, 70	.527	2.201	.021
CFE × G	12, 70	.341	4.160	<.001
P × G	24, 123	.241	2.586	<.001
CFE × P × G	24, 123	.303	2.099	.005
MANOVA 2:				
CFE	12, 36	.011	25.232	<.001
P	12, 36	.290	2.571	.014
G	6, 18	.335	5.949	.001
CFE × P	24, 64	.072	2.997	<.001
CFE × G	12, 36	.252	2.975	.006
P × G	12, 36	.321	2.299	.027
CFE × P × G	24, 64	.183	1.670	.054

Note: The traits measured included egg size, recruitment, age at maturity, size at maturity, fecundity, and adult survival. MANOVA 1 includes data from all three generations, but the current food environment treatment was simplified to just two levels (high and low) by merging the medium and low current food treatments. MANOVA 2 includes all levels of current food (H, M, L) but includes only data from generations F_1 and F_2. CFE = current food environment; P = parental environment; G = generation.

Which Traits Are Most Affected by Past Environments?

Most of the univariate analyses of individual traits demonstrated significant interactions between the effects of past environments (original parental environment and generation) and those of the current environment (table 2) and therefore support the general conclusion that life-history trait expression is the product of an interaction between past and present environments and varies from one generation to the next. Univariate analyses also demonstrated the different sensitivities of the traits measured to the effects of past and present environments. For example, the amount of variation that was attributable to the effects of the current food environment varied from 2.9% in egg length (hatched from) up to 92.2% for fecundity (table 2).

How Does the Nature of Intergenerational Effects Change in Different Environments?

Intergenerational effects must be mediated by changes in the size and provisioning of offspring that connect one generation to the next. The factor analyses shown in figure 4 demonstrate a significant change in the way that variation in egg length altered the life-history strategy of animals in different environments. For individuals experiencing high-food environments, variation in egg length predominantly influenced a negative trade-off between fecundity and adult survival and had little effect on recruitment or age and size at maturity (fig. 4*A*). In contrast, in low-food environments, variation in egg length translated into differences in the probability of recruiting and variation in age and size at maturity. However, variation in egg length did not affect either fecundity or adult survival (fig. 4*C*). Effects in medium food environments were intermediate (fig. 4*B*).

How Does the Current Food Environment Influence the Magnitude of Intergenerational Effects over Time?

The life-history strategy of animals (covariation between different life-history traits) and the way that the effects of past environments (variation in egg length) influenced life-history strategies varied in different current food environments. This affected the way that females provisioned their subsequent offspring. The results presented in figure 5 show how experimentally induced variation in egg size in the F_1 generation decreased over time in medium- and low-food environments (fig. 5*B*, 5*C*) but increased over time in high current food environments (fig. 5*A*). As a consequence, intergenerational effects eroded in medium- and low-food environments but increased in high-food

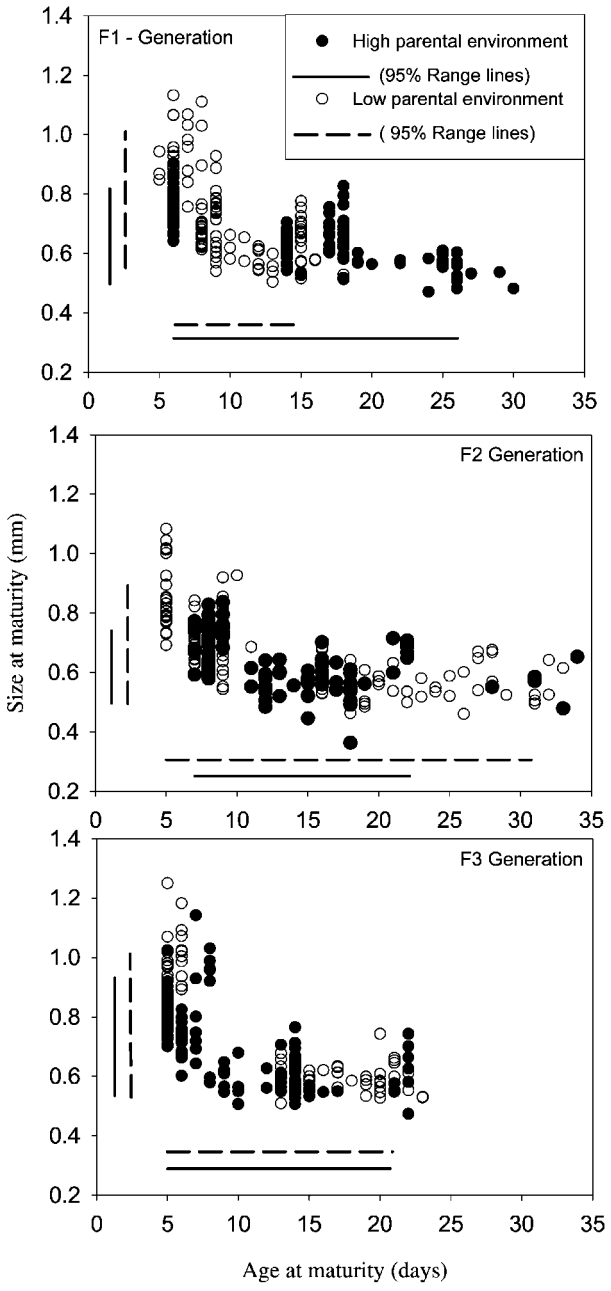


Figure 2: Effect of high and low original parental environments on the reaction norm for age and size at maturity of their offspring, grandoffspring, and great-grandoffspring. The 95% range lines for age and size are shown for high (*solid lines*) and low (*dashed lines*) parental environments. Offspring from a high original parental environment start off smaller and older at maturity than offspring from a low original parental environment in the F_1 generation (maternal effect). In the F_2 generation (grandmaternal effect), grandoffspring from low original parental environments are larger under high-food conditions but take longer to mature under low-food conditions, resulting in an expanded reaction norm compared to that of high-parental-environment grandoffspring. Finally, in the F_3 generation, the maximum and minimum ranges of size and age at maturity were similar for the two treatments, although there is clearly still a difference in distribution of the points for individuals from high and low original parental environments (see table 2 for univariate analyses of age and size at maturity). The effect of a medium original parental environment was similar to that of the low parental environment and was therefore omitted to improve the clarity of the plots.

environments. Figure 5 also clearly demonstrates how the mean size of eggs in each treatment varied from one generation to the next. The grandmaternal effect is not simply a weaker version of the maternal effect but may be stronger or even opposite in sign. An analysis of the F_2 eggs indicates that both the parental environment (in the F_1 generation) and the grandparental environment (in the P generation) influenced egg size (general linear model, effect of grandparents' food: $F = 4.76$, df $= 2, 19$, $P = .021$; effect of parents' food: $F = 4.88$, df $= 2, 19$, $P = .019$). The maternal and grandmaternal influences on egg size differed in sign, however. When grandparental food was controlled for, mothers on high food laid larger eggs than those on low food (high $= 0.1643 \pm 0.001444$ mm, low $= 0.1576 \pm 0.001680$ mm). Conversely, controlling for parental food, individuals whose grandparents had high food laid smaller eggs than individuals whose grandparents were on low food (high $= 0.1591 \pm 0.001680$ mm, low $= 0.1643 \pm 0.001444$ mm).

Discussion

By transmitting environmental conditions from past generations into phenotypic variation in subsequent generations, intergenerational effects may cause a delay in the response of a population to a change in environmental conditions (Leslie 1959; Rossiter 1994; Beckerman et al. 2002; Benton et al. 2005). In this study we show that, when a multivariate approach is adopted, an environmental perturbation that generates intergenerational effects is still detectable in the life histories of descendents three generations later (i.e., there are great-grandmaternal effects), irrespective of the food environment. However, the traits most influenced by intergenerational effects change in different food environments and from generation to generation.

In low-food environments, variation in egg size altered a trade-off between age and size at maturity and had little effect on the size of eggs produced in subsequent generations (fig. 4*C*). Consequently, the variation in egg size that drives intergenerational effects decreased over time (fig. 5*B*, 5*C*). In contrast, in high-food environments, variation in egg size predominantly influenced a trade-off between fecundity and adult survival (fig. 4*A*) and generated increasing variation in egg size (fig. 5*A*). As a result,

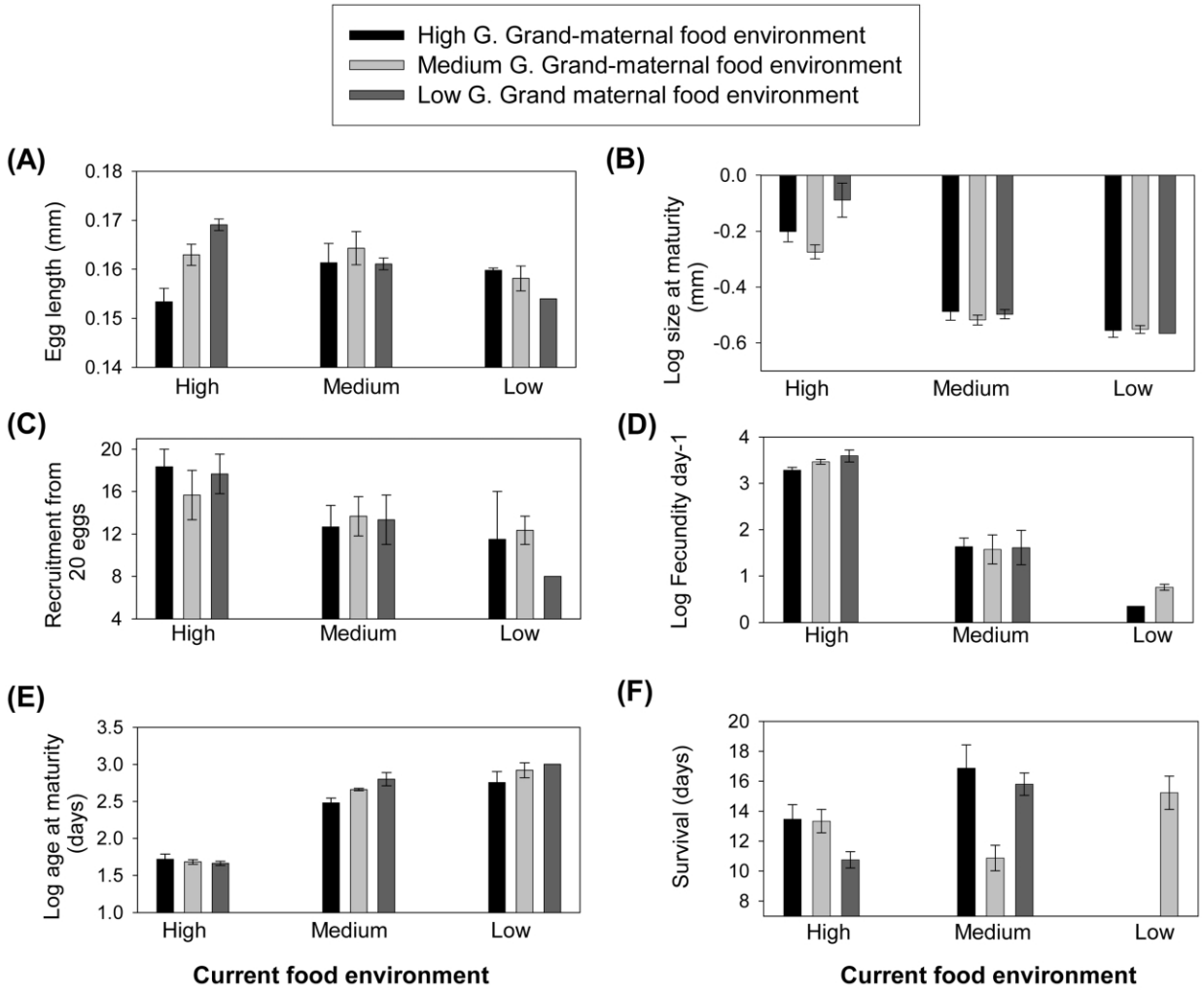


Figure 3: Variation (mean ± SE) in (*A*) egg length, (*B*) log size at maturity, (*C*) recruitment, (*D*) log fecundity per day, (*E*) log age at maturity, and (*F*) adult survival of individuals in the F_3 generation reared on either high, medium, or low current food. Great-grandmaternal food environments (original parental generation) are indicated by bar shading. Great-grandmaternal effects are apparent in some traits in some environments but not in others. Missing bars represent treatment groups that were lost before the end of the experiment.

the persistence and significance of intergenerational effects varied between high- and low-food environments (fig. 5). Our findings suggest that, in soil mites at least, the effects of past environments will be most important in populations that are not regulated by density dependence and therefore experience high current food conditions for much of the time.

Demonstrating that current environment changes the nature of intergenerational effects is not the same as demonstrating that the current environment may override intergenerational effects, as suggested in previous studies (Weiner et al. 1997; Ergon et al. 2001*a*, 2001*b*). Although this may sometimes be the case, especially in studies of plants in which propagule size is generally nonplastic (Harper et al. 1970), it is difficult to refute the possibility of context-dependent intergenerational effects without carrying out a multitrait, multienvironment study. Univariate life-history measures in single environments are likely to underestimate the full significance of intergenerational effects for a number of reasons. First, variation in any given trait may be environment dependent (Plaistow et al. 2004). Second, the influence of intergenerational effects on any single trait may be small; however, the summed effect across all traits may be biologically important. Finally, because the sensitivity of different traits to past and present environments is itself variable (table 2), the chance of detecting intergenerational effects will depend on which univariate trait is measured. Because the influence of the

Table 2: Results of general linear models

Source of variation	df	SS	*F*	*P*	η^2
Egg size:					
CFE	2	.0001	1.707	.190	2.9
P	2	.0001	2.0327	.140	3.5
G	2	.0003	5.4117	.007	9.2
CFE × P	4	.0005	4.9968	.002	17.0
P × G	4	.0005	5.3258	.001	18.1
Residual	58	.0014			49.3
Recruitment:					
CFE	2	530.10	21.9467	<.001	33.7
P	2	103.17	4.2713	.018	6.6
G	2	27.56	1.1412	.326	1.8
P × G	4	114.61	2.3724	.061	7.3
Residual	66	797.08			50.7
Age at maturity:					
CFE	2	14.8152	190.5791	<.001	74.0
P	2	.4659	5.9927	.005	2.3
G	2	.6879	8.8488	<.001	3.4
CFE × P	4	.0471	.3032	.874	.2
CFE × G	4	.3676	2.3645	.065	1.8
P × G	4	.8451	5.4357	.001	4.2
CFE × P × G	8	.8363	2.6894	.015	4.2
Residual	50	1.9434			9.7
Size at maturity:					
CFE	2	1.4829	183.5632	<.001	77.9
P	2	.0249	3.0755	.053	1.3
G	2	.0697	8.6238	<.001	3.7
CFE × P	4	.0586	3.6293	.010	3.1
Residual	66	.2666			14.0
Fecundity:					
CFE	2	133.651	642.5598	<.001	92.2
P	2	.399	1.9168	.158	.3
G	2	2.532	12.1712	<.001	1.7
CFE × P	4	1.058	2.5427	.052	.7
CFE × G	4	2.392	5.7507	<.001	1.7
Residual	47	4.888			3.4
Adult survival:					
CFE	2	94.648	8.7340	<.001	19.7
G	2	72.049	6.6486	.003	15.0
Residual	58	314.265			65.3

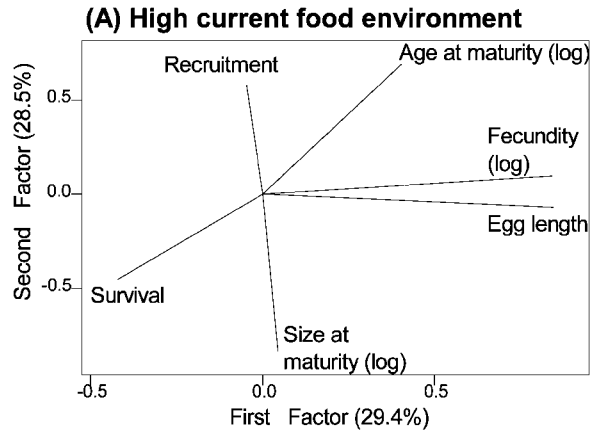
Note: Response variables were egg size, recruitment, age at maturity, size at maturity, fecundity, or adult survival, and original parental environment (high, medium, low), generation (F_1, F_2, F_3), and current food environment (H, M, L) were used as categorical explanatory variables. After fitting a full model to the data, we used a backward-stepwise procedure to remove higher-order interactions that had no significant effect. CFE = current food environment; P = parental environment; G = generation; SS = sum of squares; η^2 = percentage of total variance in each trait that is explained by each term in the model.

current environment on context-dependent phenotypic trade-offs increases with ontogeny, the effects of past environments are most likely to be observed in traits that occur early in development (Mousseau and Dingle 1991; Fox and Savalli 1998).

The context-dependent nature of intergenerational effects suggests that population models that incorporate invariable delayed life-history effects into their models (Ginzburg and Taneyhill 1994; Inchausti and Ginzburg 1998; Benton et al. 2001*a*) may be too simplistic. At present, all population models that incorporate intergenerational effects are univariate and assume that maternal quality is positively correlated with offspring quality (Ginzburg and Taneyhill 1994; Inchausti and Ginzburg 1998; Benton et al. 2001*a*; but see Benton et al. 2005 for a model with a negative correlation between mother and offspring quality). In contrast to this assumption, we found positive and negative associations between univariate measures of apparent maternal quality and offspring quality. For example, figure 4*A* shows how mothers that lay large eggs in high-food environments produce offspring that have higher fecundities but tend to die earlier. In low-food environments, mothers that lay larger eggs produce offspring that recruit better but grow at a slower rate and mature at smaller sizes (fig. 4*C*). Covariation between life-history traits may mean that a negative association between some traits (e.g., egg size and age at maturity) may reflect covariation between other traits that have a positive fitness benefit. Consequently, the way that a female provisions her offspring should depend on her own state as well as the predicted future environment, which may itself be under maternal control, as the number of offspring a mother produces will influence the competition for food experienced by each individual offspring (Bernardo 1996*a*; Benton et al. 2005).

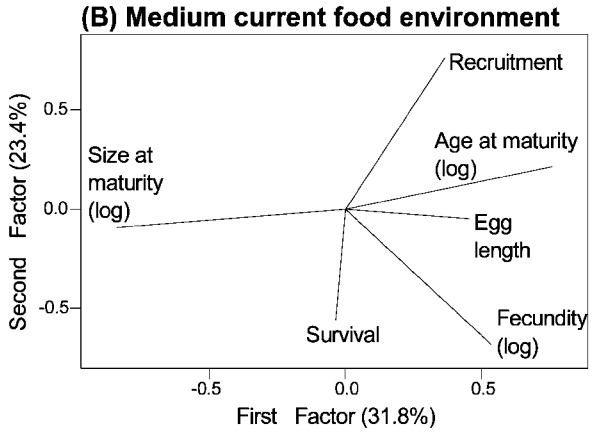
Female provisioning of eggs in *Sancassania berlesei* depends on numerous factors, including maternal body size. Since a mother's body size is itself partly determined by the size of egg that she hatched from and the conditions she experienced growing up (S. J. Plaistow, J. Grant, and T. G. Benton, unpublished manuscript), it is easy to see how interactions between intergenerational effects develop. For example, in salmon, mothers that hatch from large eggs and encounter abundant food grow to a large size but subsequently lay many small eggs. Hence, the size of eggs can flip from one generation to the next (Einum and Fleming 1999). In this study, egg sizes in the F_2 generation demonstrate an opposing effect of maternal (F_1 generation) and grandmaternal food environments (parental generation). These knock-on effects may generate transgenerational effects that are difficult to interpret (Baylis and Wiegmann 1993; Bernardo 1996*a*; Fox and Savalli 1998; Magiafoglou and Hoffmann 2003; Hunt and Brooks 2004).

Complex and context-dependent intergenerational effects on offspring performance are likely to result in complex and context-dependent effects on population dynamics. In a spatiotemporally varying world, different individuals experiencing the same environment at the same time may respond in different ways, depending on the



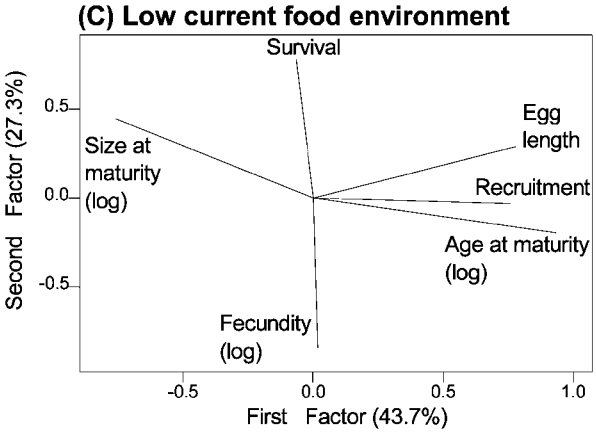
Rotated factor loadings

Variable	Factor 1	Factor 2
Mean egg length	0.844	-0.069
Mean Recruitment	-0.047	0.581
Mean Fecundity	0.841	0.099
Mean size at maturity (log)	0.044	-0.828
Mean adult survival	-0.421	-0.450
Mean age at maturity (log)	0.402	0.687



Rotated factor loadings

Variable	Factor 1	Factor 2
Mean egg length	0.455	-0.047
Mean Recruitment	0.366	0.760
Mean Fecundity	0.759	0.213
Mean size at maturity (log)	-0.841	-0.091
Mean adult survival	-0.034	-0.557
Mean age at maturity (log)	0.535	-0.680



Rotated factor loadings

Variable	Factor 1	Factor 2
Mean egg length	0.776	0.287
Mean Recruitment	0.758	-0.032
Mean Fecundity	0.017	-0.843
Mean size at maturity (log)	-0.758	0.446
Mean adult survival	-0.065	0.781
Mean age at maturity (log)	0.931	-0.196

Figure 4: Vector plots of the factor loadings for the first two factors for individuals reared in (*A*) high-food, (*B*) medium-food, or (*C*) low-food environments. Vectors that are close in space indicate positive correlation between the life-history traits. Vectors that point in opposite directions are negatively correlated, and vectors that are perpendicular are uncorrelated. The length of the vector indicates the amount of variation associated with it. *A*, In high current food environments, variation in egg length predominantly influenced a negative trade-off between fecundity and adult survival and had little effect on recruitment or age and size at maturity. *C*, In contrast, in low-food environments variation in egg length translated into differences in the probability of recruiting and variation in age and size at maturity. *B*, Effects in medium-food environments were intermediate.

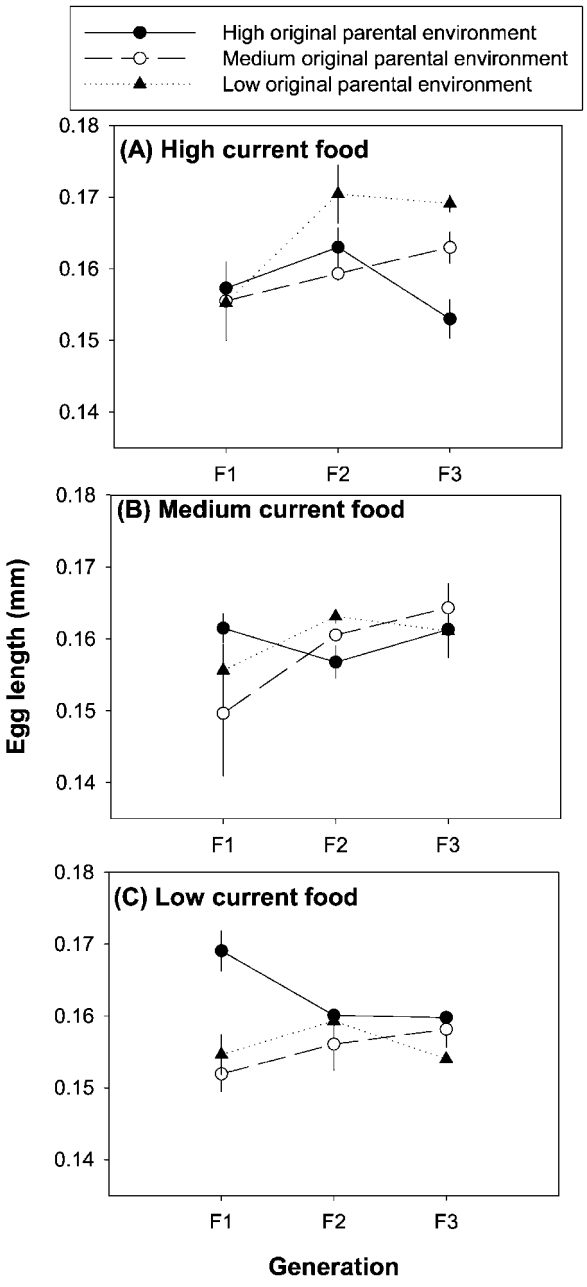


Figure 5: Change in the egg lengths (mean ± SE) used to set up treatment groups in each generation on (*A*) high, (*B*) medium, or (*C*) low current food environments. Whereas the variation in egg sizes generated in the F_1 generation gradually decreased in medium and low current food environments, it increased in high current food environments.

environments experienced by previous generation(s). For example, in soil mites, populations initiated with eggs of different mean sizes produce different population dynamics that remain distinct for multiple generations and approach an equilibrium population size in different ways (Benton et al. 2005), suggesting that subtle, context-dependent intergenerational effects are important in determining population dynamic patterns.

In conclusion, we show that an environmental perturbation can create effects that span multiple generations. The traits affected and the strength to which they are altered depend on a number of factors, such as the current environment and the number of generations since the perturbation. We particularly note that the full significance of intergenerational effects, including their context dependence, is only truly revealed when the life history is considered as a multivariate suite of traits that is then studied over multiple generations.

Acknowledgments

We thank A. Beckerman, D. Bowler, J. Fairbairn, X. Lambin, T. Marshall, and two anonymous reviewers for constructive comments that greatly improved this manuscript. Funding was provided by a Natural Environment Research Council grant (NER/A/S/2001/00430) awarded to T.G.B.

Literature Cited

Albon, S. D., T. H. Clutton-Brock, and F. E. Guinness. 1987. Early development and population-dynamics in red deer. 2. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69–81.

Andersson, M. 1978. Natural selection of offspring numbers: some possible intergeneration effects. American Naturalist 112:762–766.

Baylis, J. R., and D. D. Wiegmann. 1993. Alternating life histories of smallmouth bass. Transactions of the American Fisheries Society 122:500–510.

Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. Population dynamic consequences of delayed life-history effects. Trends in Ecology & Evolution 17:263–269.

Benton, T. G., E. Ranta, V. Kaitala, and A. P. Beckerman. 2001*a*. Maternal effects and the stability of population dynamics in noisy environments. Journal of Animal Ecology 70:590–599.

Benton, T. G., C. T. Lapsley, and A. P. Beckerman. 2001*b*. Population synchrony and environmental variation: an experimental demonstration. Ecology Letters 4:236–243.

Benton, T. G., S. J. Plaistow, A. P. Beckerman, C. T. Lapsley, and S. Littlejohns. 2005. Changes in maternal investment in eggs can affect population dynamics. Proceedings of the Royal Society of London B 272:1351–1356.

Bernardo, J. 1996*a*. Maternal effects in animal ecology. American Zoologist 36:83–105.

———. 1996*b*. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations. American Zoologist 36:216–236.

Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). Ecology 71: 1599–1608.

Bjørnstad, O. N., and T. F. Hansen. 1994. Individual variation and population dynamics. Oikos 69:167–171.

Bjørnstad, O. N., M. Begon, N. C. Stenseth, W. Falck, S. M. Sait, and D. J. Thompson. 1998. Population dynamics of the Indian

meal moth: demographic stochasticity and delayed regulatory mechanisms. Journal of Animal Ecology 67:110–126.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Czesak, M. E., and C. W. Fox. 2003. Evolutionary ecology of egg size and number in a seed beetle: genetic trade-off differs between environments. Evolution 57:1121–1132.

Dennis, B., R. A. Desharnais, J. M. Cushing, S. M. Henson, and R. F. Costantino. 2001. Estimating chaos and complex dynamics in an insect population. Ecological Monographs 71:277–303.

Einum, S., and I. A. Fleming. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. Proceedings of the Royal Society of London B 266:2095–2100.

———. 2000. Highly fecund mothers sacrifice offspring survival to maximize fitness. Nature 405:565–567.

Ergon, T., X. Lambin, and N. C. Stenseth. 2001*a*. Life-history traits of voles in a fluctuating population respond to the immediate environment. Nature 411:1043–1045.

Ergon, T., J. L. MacKinnon, N. C. Stenseth, R. Boonstra, and X. Lambin. 2001*b*. Mechanisms for delayed density-dependent reproductive traits in field voles, *Microtus agrestris*: the importance of inherited environmental effects. Oikos 95:185–197.

Fox, C. W., and U. M. Savalli. 1998. Inheritance of environmental variation in body size: superparasitism of seeds affects progeny and grandprogeny body size via a nongenetic maternal effect. Evolution 52:172–182.

Ginzburg, L. R. 1998. Inertial growth: population dynamics based on maternal effects. Pages 42–53 *in* C. W. Fox, ed. Maternal effects as adaptations. Oxford University Press, Oxford.

Ginzburg, L. R., and D. E. Taneyhill. 1994. Population cycles of forest lepidoptera: a maternal effect hypothesis. Journal of Animal Ecology 63:79–92.

Gliwicz, Z. M., and C. Guisande. 1992. Family planning in *Daphnia*: resistance to starvation in offspring born to mothers grown at different food levels. Oecologia (Berlin) 91:463–467.

Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1:327–356.

Harrell, F. 2000. The HMISC and DESIGN library for R/S-Plus. http://biostat.mc.vanderbilt.edu/twiki/bin/view/Main/RS.

Hercus, M. J., and A. Hoffman. 2000. Maternal and grandmaternal age influence offspring fitness in *Drosophila*. Proceedings of the Royal Society of London B 267:2105–2110.

Hunt, J., and R. Brooks. 2004. The mother-in-law effect. Proceedings of the Royal Society of London B 271:S61–S63.

Ihaka, R., and R. Gentleman. 1996. R: a language for data analysis and graphics. Journal of Computational and Graphical Statistics 5:299–314.

Inchausti, P., and L. R. Ginzburg. 1998. Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. Journal of Animal Ecology 67:180–194.

Kendall, B. E., S. P. Ellner, E. McCauley, S. N. Wood, C. J. Briggs, W. W. Murdoch, and P. Turchin. 2005. Population cycles in the pine looper moth (*Bupalus piniarius*): dynamical tests of mechanistic hypotheses. Ecological Monographs 75:259–276.

Lardies, M. A., M. J. Carter, and F. Bozinovic. 2004. Dietary effects on life history traits in a terrestrial isopod: the importance of evaluating maternal effects and trade-offs. Oecologia (Berlin) 138: 387–395.

Leslie, P. H. 1959. The properties of a certain lag type of population growth and the influence of an external random factor on a number of such populations. Physiological Zoology 32:151–159.

Lindstrom, J. 1999. Early development and fitness in birds and mammals. Trends in Ecology & Evolution 14:343–348.

Lindstrom, J., and H. Kokko. 2002. Cohort effects and population dynamics. Ecology Letters 5:338–344.

Livnat, A., S. W. Pacala, and S. A. Levin. 2005. The evolution of intergenerational discounting in offspring quality. American Naturalist 165:311–321.

Magiafoglou, A., and A. A. Hoffmann. 2003. Cross-generation effects due to cold exposure in *Drosophila serrata*. Functional Ecology 17: 664–672.

Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology & Evolution 16:254–260.

Mousseau, T. A., and H. Dingle. 1991. Maternal effects in insect life histories. Annual Review of Entomology 36:511–534.

Oksanen, T. A., E. Koskela, and T. Mappes. 2002. Hormonal manipulation of offspring number: maternal effort and reproductive costs. Evolution 56:1530–1537.

Parichy, D. M., and R. H. Kaplan. 1992. Maternal effects on offspring growth and development depend on environmental quality in the frog *Bombina orientalis*. Oecologia (Berlin) 91:579–586.

Plaistow, S. J., C. T. Lapsley, A. P. Beckerman, and T. G. Benton. 2004. Age and size at maturity: sex, environmental variability and developmental thresholds. Proceedings of the Royal Society of London B 271:919–924.

Räsänen, K., A. Laurila, and J. Merilä. 2005. Maternal investment in egg size: environment- and population-specific effects on offspring performance. Oecologia (Berlin) 142:546–553.

Rossiter, M. 1994. Maternal effects hypothesis of herbivore outbreak. BioScience 44:752–763.

Royama, T. 1992. Analytical population dynamics. Chapman & Hall, London.

StatSoft. 2004. Electronic statistics textbook. StatSoft, Tulsa, OK.

Stillwell, C. R., and C. W. Fox. 2005. Complex patterns of phenotypic plasticity: interactive effects of temperature during rearing and oviposition. Ecology 86:924–934.

Turchin, P. 1990. Rarity of density dependence or population regulation with lags. Nature 344:660–663.

Turchin, P., and I. Hanski. 2001. Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. Ecology Letters 4:267–276.

Weiner, J., S. Martinez, H. Müller-Schärer, P. Stoll, and B. Schmid. 1997. How important are environmental maternal effects in plants? a study with *Centaureamaculosa*. Journal of Ecology 85:133–142.

Associate Editor: Benjamin M. Bolker
Editor: Donald L. DeAngelis