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Age and size at maturity: sex, environmental variability and developmental thresholds

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In most organisms, transitions between different life-history stages occur later and at smaller sizes as growth conditions deteriorate. Day and Rowe recently proposed that this pattern could be explained by the existence of developmental thresholds (minimum sizes or levels of condition below which transitions are unable to proceed). The developmental-threshold model predicts that the reaction norm of age and size at maturity will rotate in an anticlockwise manner from positive to a shallow negative slope if: (i) initial body size or condition is reduced; and/or (ii) some individuals encounter poor growth conditions at increasingly early developmental stages. We tested these predictions by rearing replicated populations of soil mites *Sancassania berlesei* (Michael) under different growth conditions. High-food environments produced a vertical relationship between age and size at maturity. The slope became increasingly shallow as food was reduced. By contrast, high food in the maternal environment reduced the slope of the reaction norm of age and size at maturity, whereas low food increased it. Overall, the reaction norm of age and size at maturity in *S. berlesei* was significantly nonlinear and differed for males and females. We describe how growth conditions, mother's environment and sex determine age and size at maturity in *S. berlesei*.

Keywords: age and size plasticity; developmental threshold; reaction norm; *Sancassania berlesei*; growth rate; maternal effect

1. INTRODUCTION

Environmental variability is a ubiquitous feature of biological systems. Reaction norms describe the range of phenotypes expressed by a single genotype in response to these changes in the environment (Stearns & Koella 1986). Understanding the adaptive significance of reaction-norm evolution is currently a major goal for evolutionary biologists (Roff 2002). However, the study of environmentally induced variation in the expression of life-history traits also plays a key role in understanding how changes in the environment are filtered through the biology of the organisms into changes in population dynamics (Laakso *et al.* 2001; Beckerman *et al.* 2002; Lindstrom & Kokko 2002). One of the most frequently studied reaction norms is the response of size and age at maturity to changes in an individual's growth conditions (Berrigan & Charnov 1994; Twombly 1996; Morey & Reznick 2000; Day & Rowe 2002). Age and size at maturity determines not only how quickly individuals in a population can start to reproduce but also how much they can reproduce, because fecundity is often closely associated with body size (Roff 1992). Thus, the way that age and size at maturity respond to changes in the environment is likely to be a major determinant of how the population as a whole responds to environmental changes.

In a recent paper, Day & Rowe (2002) observed that, although current optimality models predict that almost any response of size and age to changes in growth rate is possible (Stearns & Koella 1986; Stearns 1992; Berrigan & Koella 1994), most organisms mature earlier and at a larger body size as growth conditions improve (Stearns & Koella 1986; Gotthard & Nylin 1995). Day & Rowe (2002) propose that the negative relationship between age and size at maturity arises because many animals have a developmental threshold, which they define as a minimum size or condition that must be exceeded before maturation (or any other transition into the next life-history stage) can occur. Using a simple optimality approach, Day & Rowe (2002) show that in the absence of a developmental threshold there is a positive relationship between age and size at maturity: as growth conditions improve, so does the fecundity advantage of delaying maturity. By contrast, in the presence of a developmental threshold the relationship between age and size at maturity becomes negative: under poor conditions, individuals grow slowly and take time to reach the threshold. At small sizes, the fecundity advantage of delaying maturity and growing past the threshold is small (see fig. 2 in Day & Rowe 2002). Accordingly, the model of Day & Rowe (2002) predicts that in poor growth conditions there should be low variation in size at maturity (all individuals mature at the minimum threshold size) but considerable variation in age at maturity. As growth conditions improve, the model predicts that there will be little variation in age at maturity, but a large variation in size at maturity. This is because poor growth conditions increase the development time prior to reaching a developmental threshold, but decrease the development time after the threshold is reached. Consequently, individuals that experience poor growth conditions can mature

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at the same age as an individual in good growth conditions, but they will do so at a much smaller size.

This model therefore makes two predictions: first, decreases in initial size will result in individuals taking longer to reach the threshold, resulting in an increasingly shallow relationship between age and size at maturity; and second, the slope of the relationship between age and size at maturity should switch from being positive in populations that experience good growth conditions to being negative or flat in populations that experience poor growth conditions. Whether the relationship between age and size at maturity is flat or negative in poor conditions will also depend upon the type of developmental threshold. A 'physical threshold' (Day & Rowe 2002) describes a minimum size or state that must be exceeded before the transition can be made. It has no effect on fecundity once it has been surpassed and therefore affects only those individuals in the population that experience poor growth conditions, generating a flat relationship between age and size at maturity in poor-growth environments. In comparison, an 'overhead threshold' (Day & Rowe 2002) describes a proportion of an individual's total resources that must be used to undergo maturation. All individuals in the population pay this cost, but its relative effect on lifetime fecundity is less for individuals in good growth conditions. Thus, in this case, the relationship between age and size at maturity is predicted to be negative in poor growth conditions and flat in extremely harsh growth conditions (see Day & Rowe (2002) for further explanation).

A recent study of the soil mite *Sancassania berlesei* (Beckerman *et al*. 2003) suggested that individuals that were reared under good growth conditions had a positive relationship between age and size at maturity, whereas animals that were reared under poor growth conditions had a negative relationship. Age at maturity increased as growth conditions decreased, and the limited data available suggested that the reaction norm between age and size at maturity is L-shaped, indicating that *S. berlesei* may have a developmental threshold.

Because *S. berlesei* is sexually dimorphic, we proposed that males and females may respond to changes in growth conditions in different ways. Sex-specific reaction norms have recently been demonstrated in a number of systems (Post *et al.* 1999; Crowley 2000; Bedhomme *et al.* 2003) and are typically attributed to differences in the growth strategies of males and females (Post *et al.* 1999; Badyaev 2002). However, male and female reaction norms may also vary in shape if males and females have different developmental thresholds. Although we know that developmental thresholds exist in numerous organisms, including insects (Moed *et al.* 1999), crustaceans (Ebert 1994), amphibians (Morey & Reznick 2000) and flowers (Wesselingh *et al.* 1997), and may vary between species (Morey & Reznick 2000) or between different genetic lines of the same species (Wesselingh *et al.* 1997), sex differences in the position of a developmental threshold have, to our knowledge, never previously been tested for.

The *S. berlesei* system is ideal for testing the predictions from Day and Rowe's developmental-threshold model because all animals are reared in controlled predator-free environments, so any effect that predation risk might have on growth rates (Lima & Dill 1990) is removed. We reared replicated populations of *S. berlesei* from different maternal backgrounds across a range of environmental conditions to determine how maternal environment, growth conditions and sex interact to determine age and size at maturity in this species. A separate experiment in which we reared individual males and females on *ad libitum* food was used to test whether male and female *S. berlesei* have different growth rates.

2. MATERIAL AND METHODS

(a) *Study organism*

The *S. berlesei* used in these experiments were taken from a laboratory culture that was originally collected from an agricultural manure heap in 1996 and 1998. Details regarding the maintenance of the stock culture, basic experimental techniques and information about the basic biology of *S. berlesei* can be found elsewhere (Benton *et al.* 2001).

(b) *Experimental design*

(i) *Reaction norm of age and size at maturity*

The data used in this analysis come from an experiment that was designed to measure the strength and the duration of maternal effects. A total of 640 eggs were collected from second-generation females from replicated common garden cultures. Eggs were collected from a single 24 h laying period and then randomly divided into batches of 20, and reared in 34 identical culture tubes (Benton *et al.* 2001). All the tubes were fed and watered once a day. Food consisted of a 'hole punch' disc of filter paper (diameter of 6 mm) onto which a drop of yeast solution had previously been dropped and left to dry in an oven. We used 0.5, 0.06 and 0.02 mg 10 ml^{-1} yeast solutions as high, medium and low *parental* food treatments (determined from preliminary trials). Six of the 34 tubes were fed high-food, six were fed medium-food and 22 were fed low-food diets. All of the tubes were checked once a day, and, upon maturation, adults were removed from the tubes and sorted into new tubes containing 10 males and 10 females from the same feeding regime. Eggs that were 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 each 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). Each treatment consisted of between three and 22 replicates. We recorded the sex and age at maturity (to the nearest day) of all individuals maturing from three replicates within each treatment. Newly matured animals were photographed using a Canon Powershot S40 digital camera connected to a Vision Engineering 'Lynx' head-up stereomicroscope. 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 (http://rsb.info.nih.gov/ij). Individuals maturing from surplus replicate tubes within each treatment were used as 'back-ups' to ensure that we had sufficient numbers to set up subsequent generations. The experiment was continued for a further two generations on the same *offspring* feeding regimes (i.e. HHHH, HMMM, HLLL, MHHH, MMMM, MLLL, LHHH, LMMM, LLLL). We analysed the relationship between age and size at maturity using a linear mixed-effects model with ln(size) as the dependent variable and ln(age) as a continuous covariate. Treatment was fitted as a nine-level factor, generation was fitted as a three-level factor and sex was fitted as a two-level factor. Tube (1, 2, 3) was included as a random factor, nested within

treatment. After fitting a full model to the data, we used a backwards stepwise procedure to remove interactions that had no significant effect.

(ii) *The effects of sex*

To examine in more detail how the reaction norm of age and size at maturity differs between males and females we used the S-PLUS statistical software to fit a variety of nonlinear least-squares models to the data. These were then compared and the model with the lowest residual standard error was selected. The interaction between 'sex' and each coefficient in the chosen model was then tested individually using an *F*-test to determine whether incorporating a sex difference in the value of the coefficient explained a significantly greater proportion of the variance than a model in which no sex interaction was included (S-PLUS 6 for windows, Guide to Statistics, 2001).

(iii) *Male and female growth rates*

In a separate experiment, we isolated eight females from a well-fed background population (two 0.100–0.125 mm balls of yeast a day for 200–300 individuals for several generations) and eight females from our stock cultures (low-food conditions) and placed each group of eight females into a separate culture tube with *ad libitum* food for 24 h. Single eggs from the 'stock' females ($n = 53$) and the 'well-fed' females ($n = 47$) were then placed into individual 1 cm × 2 cm × 2 cm plastic tubes half filled with plaster of Paris. The length of each egg was measured to the nearest 0.015 mm using an eyepiece graticule in a Leica MZ8 binocular microscope. Each egg tube was supplied with *ad libitum* food and sealed with cling film. Tubes were checked each day and the length of the developing individual in each tube was re-measured as the distance from the tip of the hypostome to the tip of the opisothoma, using the technique described for measuring eggs. Not all individuals were visible on all days so some measurements were missed. We recorded the sex of each individual and their final size at maturation. The growth rates of the different treatment groups were compared using a linear mixed-effects model with length as the response variable. Fixed effects included day as a covariate, and sex and parental background as two-level fixed factors. Individual was nested within day and included as a random effect (Crawley 2003).

3. RESULTS

(a) *Reaction norm of age and size at maturity*

Overall the shape of the reaction norm for age and size at maturity fits very closely to the L-shape predicted by the developmental-threshold model of Day & Rowe (2002) (figure 1). The relationship between log(age) and log(size) differed significantly depending upon treatment group (table 1), suggesting that age and size at maturity are affected by current and maternal growth environments. Figure 2*a* demonstrates how the slope of a line drawn between the largest individual observed in the experiment (maximal growth conditions) and the median aged and sized individual in each treatment becomes increasingly shallow as food availability is reduced and increasing numbers of individuals are forced to delay maturity and to mature at the minimum threshold size. By contrast, figure 2*b* shows how having a mother from a poor-growth environment resulted in offspring having a steeper relationship between age and size at maturity than did the offspring of mothers that had experienced good growth conditions. The significant interaction between treatment and generation arises from changes in juvenile growth rates that are caused by changes in the maternal allocation of resources to eggs and lead to different ages and sizes at maturity.

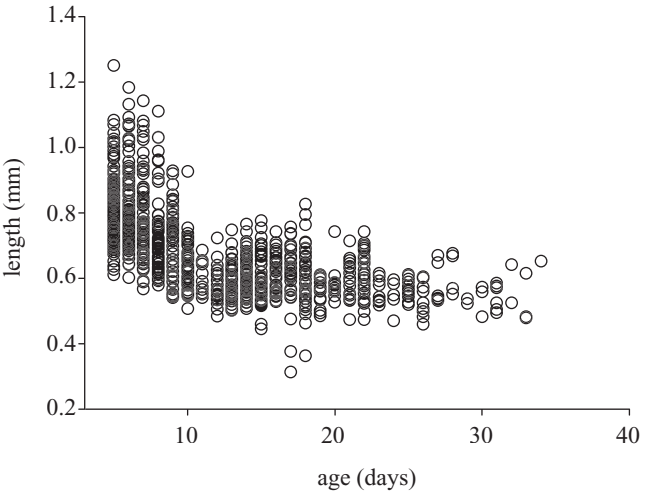

Figure 1. Reaction norm of age and size at maturity for the soil mite *Sancassania berlesei*.

Table 1. A general linear model testing for factors that influence ln(size at maturity).
(Treatment, sex and generation were all included in the model as fixed factors, ln(age) was entered as a covariate and tube was included as a random factor nested within treatment.)

source	d.f.	MS_{adj}	*F*	*p*
log(age)	1	0.25763	26.65	0.001
treatment	8	0.01799	1.81	0.072
tube (treatment)	18	0.06353	6.57	0.001
sex	1	0.03458	3.58	0.059
generation	2	0.40551	41.95	0.001
treatment × log(age)	8	0.03152	3.26	0.001
treatment × generation	16	0.06811	7.05	0.001
error	901	0.00967		
total	955			

(b) *The effects of sex*

The average reaction norm between age and size at maturity was best described by an asymptotic negative exponential decay function

$$\text{size at maturity} = a + b \times e^{(-c \times \text{age at maturity})},$$

where *a* is the asymptote of the curve (estimated developmental threshold), $a + b$ is the estimated *y*-axis intercept (for simplicity we will refer to *b* as the *y*-axis intercept in the model) and *c* is the rate of decay. All the coefficients differed significantly from 0 for both males ($a = 0.568 \pm 0.007$, $t = 78.22$; $b = 0.839 \pm 0.126$, $t = 6.67$; $c = 0.260 \pm 0.030$, $t = 8.59$) and females ($a = 0.558 \pm 0.019$, $t = 29.30$; $b = 0.601 \pm 0.052$, $t = 11.50$; $c = 0.142 \pm 0.023$, $t = 6.16$). The rate of decay of the female slope (*c*) was significantly different from that of the male slope ($F_{\text{sex} \times c;1,951} = 9.45$, $p = 0.002$; figure 3), and there was a

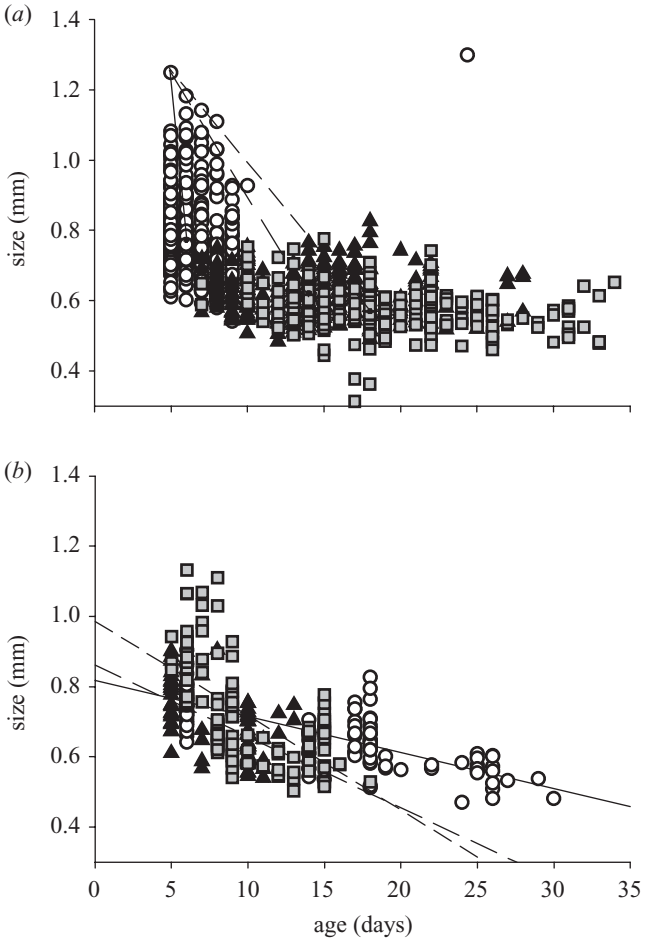

Figure 2. (*a*) The effect of good (circles and solid line), medium (triangles and long-dashed line) or poor (squares and short-dashed line) growth conditions on the slope of a line drawn between the largest individual observed in the experiment (maximal growth conditions) and the median aged and sized individual in each treatment. (*b*) The effect of maternal environment on the slope of the reaction norm of age and size at maturity (high-food slope, $y = 0.818 \pm 0.0103x$ (circles and solid line); medium-food slope, $y = 0.861 \pm 0.020x$ (triangles and long-dashed line); low-food slope, $y = 0.986 \pm 0.0268x$ (squares and short-dashed line)).

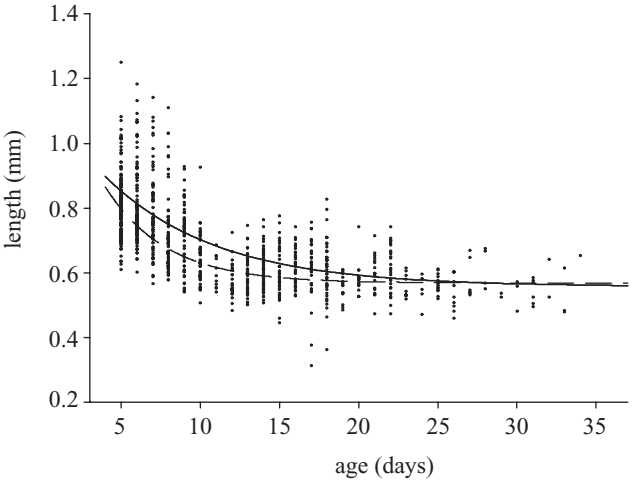

Figure 3. Average male (dashed line) and female (solid line) ages and sizes at maturity in *Sancassania berlesei*. The lines were fitted using nonlinear regression techniques in S-PLUS to fit the model size at maturity = $a + b \times e^{(-c \times \text{age at maturity})}$, where a is the asymptote of the curve (male = 0.568 ± 0.007; female = 0.558 ± 0.019), b is the estimated y-axis intercept (male = 0.839 ± 0.126; female = 0.601 ± 0.052) and c is the rate of decay (male = 0.260 ± 0.030; female = 0.142 ± 0.023).

marginally non-significant difference in the estimated y-axis intercepts (b) for male and female curves ($F_{\text{sex} \times b;1.951} = 3.27$, $p = 0.071$; figure 3). However, there was no difference in the asymptote or the average developmental threshold (a) of the male and female reaction norms ($F_{\text{sex} \times a;1,951} = 0.38$, $p = 0.53$; figure 3).

(c) *Male and female growth rates*

In the individual rearing experiment there was no difference in the growth rates of males and females (log(day) × sex: male coefficient = 0.760, female coefficient = 0.787, d.f. = 283, $t = -0.962$, $p = 0.337$; figure 4*a*); however, individuals with poorly-fed parents grew faster than individuals with well-fed parents (day × background: well-fed coefficient = 0.724, poorly fed coefficient = 0.829, d.f. = 283, $t = -2.83$, $p < 0.01$; figure 4*b*).

4. DISCUSSION

In this experiment we have described how growth conditions and sex interact to determine age and size at maturity in the soil mite *S. berlesei*. The L-shaped reaction norm fits well with the predictions of the developmental-threshold model of Day & Rowe (2002). Age and size at maturity were strongly influenced by growth conditions: mites that were reared in poor growth conditions were half the size of mites that were reared under good growth conditions and took up to five times longer to develop (figure 1). We suggest that this is because in the high-food treatment all individuals generally had sufficient food to develop past the developmental threshold, therefore food limitation became important only after the developmental threshold had been crossed, if at all. As a result, most of the variation among individuals is expressed as differences in body size and there is little variation in the age at which individuals mature. By contrast, in the low-food treatments, poor growth conditions immediately after hatching forced the mites to continue to grow until the threshold size was reached. The fastest of these 'slow-growing' individuals delayed maturity slightly upon reaching the threshold, but most poorly-fed individuals matured immediately. As a result, there is considerable variation in the time taken to reach the threshold size but little variation in body size. The negative slope between age and size at maturity demonstrated by mites reared under poor feeding conditions (figure 2*a*), suggests that in *S. berlesei* age and size at maturity are determined by an overhead threshold that affects all individuals, rather than a physical threshold that would have affected only slow-growing individuals and would have resulted in an invariant size at maturity for individuals from the poorly fed treatments (see Day & Rowe 2002).

We found no difference in the predicted positions of male and female developmental thresholds, although both

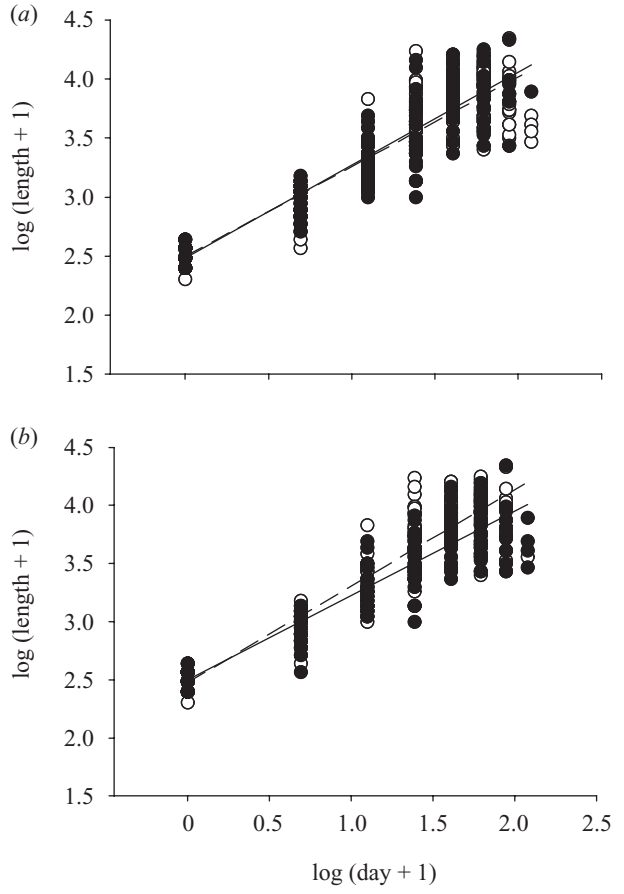

Figure 4. The effects of (*a*) sex on the growth rate of isolated eggs reared on *ad libitum* food (male slope, $y = 14.20 + 6.49x$ (open circles and dashed line); female slope, $y = 12.11 + 7.58x$ (filled circles and solid line)), and (*b*) maternal environment on the growth rate of isolated eggs reared on *ad libitum* food (high-food slope, $y = 13.52 + 6.15x$ (filled circles and solid line); low-food slope, $y = 13.00 + 7.87x$ (open circles and dashed line)).

the rate of decay and, to a marginal extent, the *y*-axis intercept of the female reaction norm were significantly lower than those of males (females are larger than males) suggesting either, that in *S. berlesei* females grow at a faster rate than males, or that under certain conditions they grow for longer. Given that we found no difference in the growth rates of individually reared males and females, we suggest that the second explanation is more probable. Since larger females lay more eggs in this species (Beckerman *et al.* 2003), a delayed age at maturity in females is probably the result of selection for increased fecundity.

The differing responses of males and females to changes in growth conditions determined the degree of sexual dimorphism. Figure 3 shows how, under poor growth conditions, there is little sexual dimorphism in body size; however, sexual dimorphism increases as growth conditions improve. Sex-specific responses to changes in environmental conditions have previously been demonstrated in numerous systems (Sergey & Gerson 1995; Post *et al.* 1999; Bedhomme *et al.* 2003) and may have important implications for understanding variation in population sex ratios.

The growth experiment revealed an effect of the maternal rearing environment on offspring growth rates: offspring from mothers reared in poor environments grew faster than offspring from mothers reared in good environments. Evidence that maternal effects can influence offspring performance is now becoming widespread (Rossiter 1996; Mousseau & Fox 1998). However, it has more recently been suggested that some maternal effects are examples of adaptive transgenerational plasticity, whereby females use current environmental cues to alter their offspring-investment strategies in a manner that increases their fitness (Mousseau & Fox 1998; LaMontagne & McCauley 2001; Rotem *et al.* 2003). If female *S. berlesei* use low food as a cue for harsh conditions, it would make sense for them to lay fewer better-provisioned eggs that grow faster and are more likely to survive. By contrast, we would expect them to lay a greater number of less-well-provisioned eggs if they experience good food conditions, since it is less likely that their offspring will struggle to survive. This sort of adaptive plasticity in egg provisioning has previously been demonstrated in a number of other arthropods (Fox & Czesak 2000), and may explain how differences in a female's environment are transmitted into differences in the growth rates of her offspring, as we observed here. Figure 2*b* shows how these maternally derived effects can influence age and size at maturity in *S. berlesei*.

The existence of the L-shaped reaction norm has important consequences for population dynamics in variable environments. If individuals are well fed, they will grow fast and mature at a larger body size. Consequently, females can lay a large number of eggs (Roff 1992). Large numbers of eggs from a cohort of well-fed mothers will lead to large numbers of juveniles that suffer from the effects of strong competition. Hence, these juveniles may grow slowly and mature at a small size, with low fecundity. This response of fecundity to food, mediated by competition and growth rates, is a potential mechanism for overcompensating density dependence in a variable environment.

We have shown that in the soil mite *S. berlesei* the trade-off between age and size at maturity is extremely plastic and is strongly influenced by growth conditions. In favourable environments, the relationship between age and size at maturity is best described as a vertical line, whereas in poor environments the relationship tends to be negative becoming increasingly shallow as growth conditions deteriorate. Overall, the shape of the reaction norm is best described by a negative exponential function that conforms to the L-shape predicted by the developmental-threshold model of Day & Rowe (2002). Males and females have the same developmental threshold, although there is some evidence that females may grow for longer under certain environmental conditions, resulting in an increase in the degree of sexual dimorphism with improving growth conditions. Offspring from mothers reared in poor environments grow faster than offspring from mothers reared in favourable environments suggesting maternal effects. We suggest that, in *S. berlesei*, age and size at maturity are ultimately the result of an interaction between the mother's growth environment, current growth conditions and sex.

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