How to Put All Your Eggs in One Basket: Empirical Patterns of Offspring Provisioning throughout a Mother's Lifetime

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ABSTRACT: Maternal effects arise when a mother's phenotype or the environment she experiences influences the phenotype of her progeny. Most studies of adaptive maternal effects are a "snapshot" of a mother's lifetime offspring provisioning and do not generally consider the effects of earlier siblings on those produced later. Here we show that in soil mites, offspring provisioning strategies are dynamic, changing from an emphasis on egg number in young females to egg size in older females. This pattern may be adaptive if it increases the survival of younger offspring that must compete with older, larger siblings. The dynamic shift in egg provisioning was greater in high-food environments in which females lived longer, creating increasing asymmetry in offspring competitive abilities. Females reared in isolation and in the presence of a high-density colony had identical provisioning strategies, suggesting that, unlike males in this species, females do not use pheromones to assess colony size. Our findings suggest that the adaptive significance of maternal effects may be misinterpreted when studies consider only a snapshot of a female's offspring provisioning strategy or when components of the offspring provisioning strategy are studied in isolation.

Keywords: maternal effects, reproductive effort, sibling rivalry, fitness, adaptive death.

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Maternal effects arise when a mother's phenotype and/or the environmental conditions she is exposed to influence the phenotype of her progeny (Falconer 1989; Mousseau and Fox 1998*a*, 1998*b*). Variation in propagule or progeny size is the "classic" maternal effect in ecology and has been shown to influence an array of different offspring characteristics (Mousseau and Fox 1998*b*). By changing progeny phenotypes, maternal effects can influence evolutionary responses (Kirkpatrick and Lande 1989, 1992; Cheverud and Moore 1994; Wade 1998) and may also drive population dynamic changes (Rossiter 1994, 1995; Benton et al. 2005).

Given the evolutionary and ecological consequences that maternal effects can have, interpreting their adaptive significance has become increasingly important. In many cases, this involves demonstrating how variation in propagule or progeny size influences the fitness of offspring in different environments (Mousseau and Fox 1998*b*). However, maternal effects are not just related to changes in propagule size. The frequent phenotypic trade-off between progeny number and progeny size (Roff 1992; Stearns 1992) means that when mothers alter their per offspring investment, they may also simultaneously alter the competitive environment that those progeny experience (Park 1935; Glazier 1998; Messina 1998). In viscous populations with overlapping generations, mothers and offspring compete for the same resources and may therefore directly influence each other's probability of survival and future reproductive success. When fecundity declines with maternal age, offspring dispersal is limited, and relatedness among conspecifics is high enough, kin selection might even drive the evolution of adaptive maternal death (Travis 2004; Dytham and Travis 2006). For example, in the social spider *Diaea ergandros*, mothers store food in trophic oocytes and are subsequently eaten by their offspring (Evans et al. 1995); however, this behavior does not occur when immigration decreases the relatedness of the brood (Evans 1998).

Covariation between offspring quality or size, offspring number, and female survival means that a change in one offspring provisioning trait may often generate changes in

the others. Consequently, an understanding of how females change their offspring provisioning strategy as a whole, in response to changes in their environment and/or condition, may be necessary to fully interpret the adaptive significance of maternal effects. Most studies of adaptive maternal effects are a "snapshot" of a mother's lifetime offspring provisioning strategy. As such, they generally do not consider the fitness consequences that the observed offspring may have on siblings produced before or after the current bout of reproductive investment. Older offspring often help to rear subsequent young in cooperatively breeding species (Stacey and Koenig 1990). However, in other systems, older offspring may deplete resources (Park 1935; Falconer 1965; Beckerman et al. 2005) or even increase the risk of mortality through cannibalism (Elgar and Crespi 1992; Perry and Roitberg 2005; Cameron et al. 2007) or siblicide (Mock and Parker 1997). Offspring therefore often change the environment that their siblings experience. In this case, selection should favor mothers that provision their offspring in a way that reduces the negative fitness consequences that offspring have on each other (Parker and Begon 1986; Mock and Parker 1997). For example, in the housefly *Musca domestica*, later offspring laid by older females are better larval competitors at high density than offspring laid by younger females (McIntyre and Gooding 2000). Likewise, in some bird species, the degree of hatching asynchrony can influence the severity of competition that nestlings endure. In brood-reducing species, mothers may even increase sibling rivalry in order to ensure that at least one offspring survives a harsh environment (Mock and Parker 1997). Alternatively, in the burying beetle *Nicrophorus orbicollis*, mothers use filial cannibalism to regulate brood size according to the size of carcass on which eggs are laid (Creighton 2005).

Even when offspring do not directly compete for resources in the same environment, the provisioning of offspring at different stages in a female's lifetime may still not be independent, because investment in earlier offspring may alter the resources left to provision later offspring. For example, in some endopterygote insects, a finite source of energy is used to provision offspring, and egg size declines as females age and resources become limited (Dixon et al. 1993; Fox and Czesak 2000). Similarly, in some mammal species, increased investment in offspring one year can alter the survival probability of subsequent offspring (Clutton-Brock et al. 1981; Berube et al. 1996). In other species, the number of offspring left to produce or the time left to produce them may be limiting (Thorne et al. 2006). The point is that the maternal effects often documented in other studies may be only part of a female's lifetime offspring provisioning strategy. Ignoring this may either overestimate or underestimate the adaptive significance of any maternal effect.

Although many studies have shown that larger females generally possess larger gametic masses, studies that examine the lifetime allocation of these resources between individuals clutches and individual eggs in females of different sizes are rare (Parker and Begon 1986). As a result, our understanding of how females alter their overall offspring provisioning strategy (egg number, egg size over the course of their lifetime) in response to changes in their environment and/or state is limited. The rapid generation time of the soil mite *Sancassania berlesei* (approximately 10 days on high food) make this species an ideal system in which to study lifetime offspring provisioning strategies. We carried out a factorial experiment to examine how the lifetime offspring provisioning strategies (egg size, egg number, maternal survival) of individual female soil mites changed in response to changes in their developmental environment (body size) and their adult food environment. In *S. berlesei*, males use a pheromone cue to assess colony density and determine whether they should develop as fighter males or nonfighter males (Radwan 1993; Radwan et al. 2002). Consequently, in a second experiment, we used a manipulation of a colony pheromone cue to test the hypothesis that perceived levels of competition influence a female's lifetime offspring provisioning strategies.

Material and Methods

Study System

The *Sancassania berlesei* used in these experiments were taken from a laboratory culture that was originally collected from an agricultural manure heap in 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).

Experiment 1: Food and Offspring Provisioning Strategies (Fig. 1)

Step 1. In order to obtain a cohort of eggs of identical age, 20 females were removed from a well-fed common-garden tube (six balls of yeast a day for 200–300 individuals for several generations) and placed into several fresh culture tubes with ad lib. food for 24 h.

Step 2. Eggs laid during the 24-h period were used to set up 22 identical culture tubes (Benton et al. 2001), each containing 20 randomly chosen eggs. All tubes were checked daily, and once 10 or more eggs had hatched in a tube, it was allocated to one of three "rearing" treatments designed to produce individuals of different size with different developmental environments. Five tubes were fed a
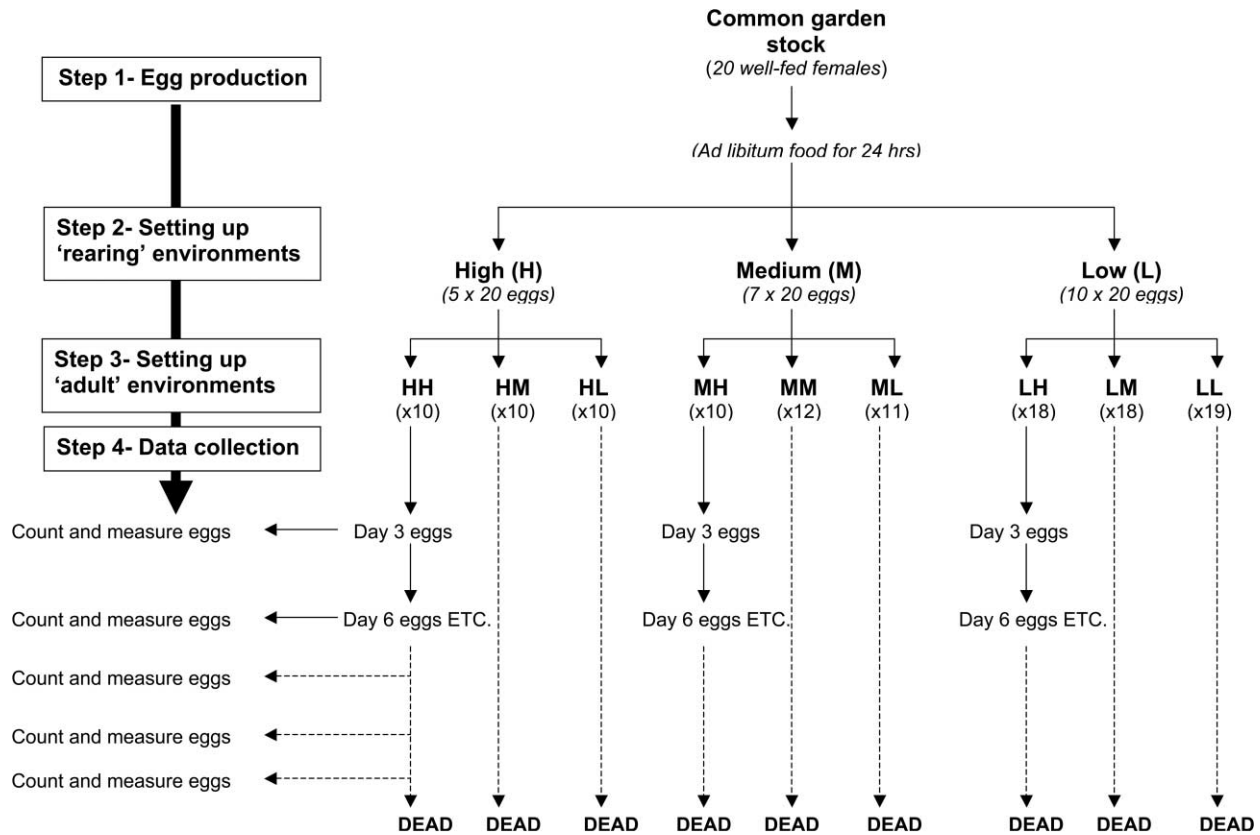
Figure 1: Schematic explaining the multiple steps carried out during experiment 1.

high-food diet consisting of ad lib. balls of yeast, seven tubes were fed a medium diet of one ball of yeast a day (1.12 ± 0.2 [SD] mg), and 10 tubes were fed a low-food diet of one rod of yeast a day (0.142 ± 0.01 [SD] mg). Excess food was removed each day to ensure that food levels remained constant throughout the experiment. Tubes were checked twice a day for newly matured adults. Males were discarded, whereas newly matured females were photographed using a Canon Powershot S40 digital camera connected to a Vision Engineering Lynx stereo-microscope at ×40 magnification. Length was measured as the distance from the tip of the hypostome to the tip of the opisthosoma.

Step 3. Newly eclosed females from each of the rearing treatments were then placed into individual plastic vials (diameter 1 cm, height 3 cm) containing a plaster base moistened with blue food coloring in order to darken the substrate. We added two males from a group of 150 males that had been fed ad lib. and kept as a single-sex culture for at least 2 days. This ensured that all males used in the experiment had similar rearing environments and had not

recently mated. In order to cross rearing treatment with adult food treatment, trios of one female and two males were then alternately allocated to one of three "adult" feeding regimes: high food (ad lib. balls), medium food (half a rod of yeast, 0.060 ± 0.006 [SD] mg), or low food (a speck of yeast, 0.036 ± 0.005 [SD] mg); the tubes were sealed with cling film and kept in an incubator at 24°C.

Step 4. Each tube was fed and watered daily, and the females were checked to see whether they were alive. Every third day, females were transferred to a fresh tube with two fresh males, and the eggs they had laid in the previous 3 days were counted and photographed as above. A random sample of 10 eggs was measured from tip to tip using the ImageJ 1.28u image analysis package (http://rsb.info.nih.gov/ij) in order to determine the average size of egg laid at this time. The mean per capita fecundity per day was calculated as the total number of eggs divided by the number of days the female was alive for during the 3-day period. Lifetime reproductive output was defined as the sum of egg number × egg size for each 3-day period.

Experiment 2: Pheromone Cues and Offspring Provisioning Strategies

The second experiment used a design similar to the first, but with cross-factored "food" and "exposure to colony pheromone" treatments instead of rearing-food and adult-food treatments (see fig. 1).

Step 1. A cohort of eggs laid within a 24-h period was obtained using the same methodology described in experiment 1 (see above).

Step 2. Two-hundred eighty eggs were selected at random from the egg collection tubes and allocated in batches of 20 to 14 fresh plaster-based tubes (Benton et al. 2001). As in experiment 1, when 10 eggs had hatched, an ad lib. diet of yeast was supplied to the growing larvae. Females ($n = 84$) that matured within a 24-h period were removed and placed in individual plastic vials with a fine nylon mesh lid. With each female were placed two virgin males collected from a single-sex culture fed ad lib. for at least 2 days. Each newly matured female was given an identification number, photographed, and measured as in experiment 1 and randomly allocated to one of four experimental treatment groups: high food with colony pheromone (H + P), low food with colony pheromone (L + P), high food with no colony pheromone (H − P), low food with no colony pheromone (L − P). There were 21 individuals in each treatment group.

Step 3. Adult food levels consisted of a high-food treatment (ad lib. yeast balls) and a low-food treatment (a speck of yeast, 0.036 ± 0.005 [SD] mg) every other day. Exposure to colony pheromone was manipulated by dividing the females' individual vials between two Tupperware containers, one of which (colony pheromone) contained a large pot containing a dense stock culture and the other of which (no colony pheromone) contained an identical pot with no culture. These Tupperware containers were kept on the same shelf of an incubator at 24°C.

Step 4. Every day, we checked each female and recorded any deaths. Any dead males were replaced with fresh ones, and all tubes were given one drop of water. Every other day, females were transferred to a fresh tube and supplied with two fresh males. Eggs laid during this time were counted and measured as in experiment 1.

Statistical Analysis

Offspring provisioning strategies of females in different treatment groups were compared using linear mixed-effects models with mean egg length and fecundity (per 3 days) as response variables and age and body size fitted as continuous covariates. Rearing food (H, M, L), adult food (H, M, L), and pheromone treatment (present, absent) were fitted as factors, and individual was fitted as a random factor. We used likelihood ratio tests (LRTs) to test for a significant effect of random intercepts and slopes for individuals. Random slope terms were removed from the model if they were not significant (tests not shown); however, all models included random intercept terms in order to control for repeated measurements taken from the same individual (Crawley 2002). In order to examine the covariation between egg number and egg size, we refitted the egg size model described above with fecundity included as a covariate. To compare the mean survival probability (age at death) of females in the two experiments, we fitted parametric accelerated failure time models using the "psm" function in the "Design" package in R (Ihaka and Gentleman 1996; Harrell 2000). Body size was fitted as a continuous explanatory variable, with adult food treatment fitted as a three-level factor (H, M, L) and colony pheromone treatment fitted as a two-level factor (present, absent). Finally, factors influencing total lifetime reproductive effort were compared using a general linear model with body size and age at death fitted as covariates and adult food treatment fitted as a three-level factor (H, M, L). 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. Model selection was based on the Akaike Information Criterion. All models are presented with degrees of freedom and LRT statistics. All P values are based on χ^2 Wald tests.

Results

Experiment 1: Egg Size and Fecundity

Larger females generally laid larger eggs than smaller females, although the strength and direction of this effect varied according to rearing background; egg size decreased slightly with increasing female size in females on a low-food rearing diet (LRT rearing food × size = 7.14, df = 2, $P = .0282$). Egg size increased as females got older, but not as much in females on a low-food adult diet (fig. 2, *top*; LRT adult food × age = 8.95, df = 2, $P = .0114$). Fecundity was explained by a three-way interaction between rearing diet, adult diet, and female age (LRT rearing food × adult food × age = 20.6, df = 4, $P < .0004$). Females with access to more food laid more eggs. Fecundity declined with age in all females, although the rates of decline depended on the combination of rearing food and adult food available to females (see fig. 2, *bottom*). After both rearing food and adult food were fitted in the model, there were no further effects of body size on fecundity (LRT size = 0.4, df = 1, $P = .541$). In the second analysis, in which fecundity was included in the egg size model as a covariate, there was still a positive effect of female body size on egg size, with effects that varied according
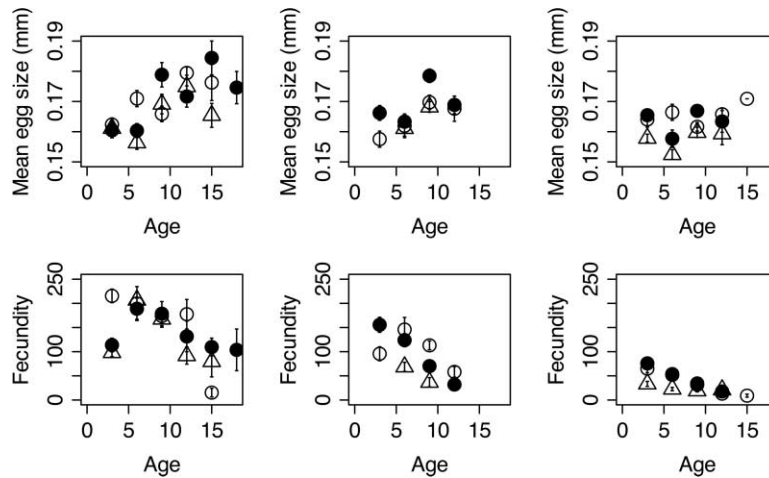
Figure 2: Effect of female age on the size of egg (mean ± SE) a mother lays in high-, medium-, and low-food environments (*top*, *left to right*), and the number of eggs a mother lays in 3 days (mean ± SE) in high-, medium-, and low-food environments (*bottom*, *left to right*). The symbols refer to females reared in high-food (*filled circles*), medium-food (*open circles*), and low-food (*triangles*) conditions.

to rearing background (LRT size = 8.83, df = 2, P = .0121). However, in low-food environments, young females that laid larger eggs also laid more eggs, whereas in medium- and high-food environments, egg size was negatively correlated with fecundity (fig. 3a; LRT food × fecundity = 6.56, df = 2, P = .0376). As females aged, the relationship between egg size and fecundity became increasingly positive in all food environments for females of all sizes (fig. 3b; LRT age × fecundity = 7.81, df = 1, P = .0051). These results suggest that while body size determines the range of egg numbers and egg sizes a female may lay during her lifetime, the exact nature of offspring provisioning is both context dependent (food availability) and dynamic (female age).

Experiment 1: Age at Death

Females with more adult food generally survived longer (LRT adult food = 14.95, df = 2, $P < .001$). The effect of food on female age at death was most apparent for larger females (fig. 4), although the interaction between adult food and female body size was marginally nonsignificant (LRT adult food × size = 5.36, df = 2, P = .069).

Experiment 1: Lifetime Reproductive Output

Lifetime reproductive effort increased with age at death in all females (fig. 5); however, the significance of age at death varied for females reared in different food envi-
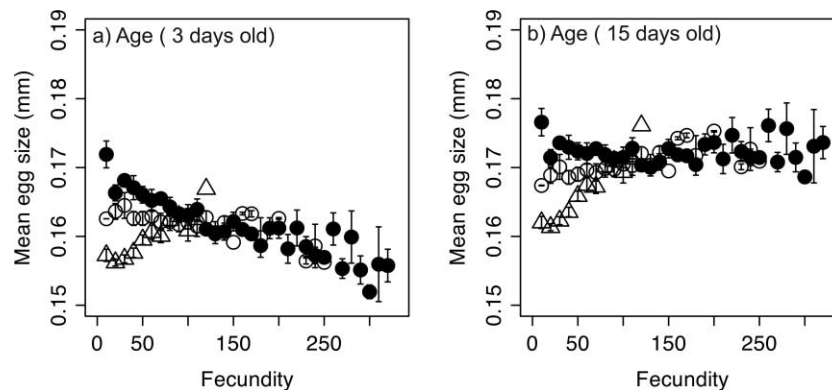

Figure 3: Predicted relationship between fecundity and egg size for young (3 days old; *a*) and old (15 days old; *b*) females in high (*filled circles*), medium (*open circles*), and low (*triangles*) adult food environments. Each point represents the mean ± SE predictions of the best-fitting linear mixed-effects model (see "Results"), after rearing food environment, body size, and random effects are controlled for.
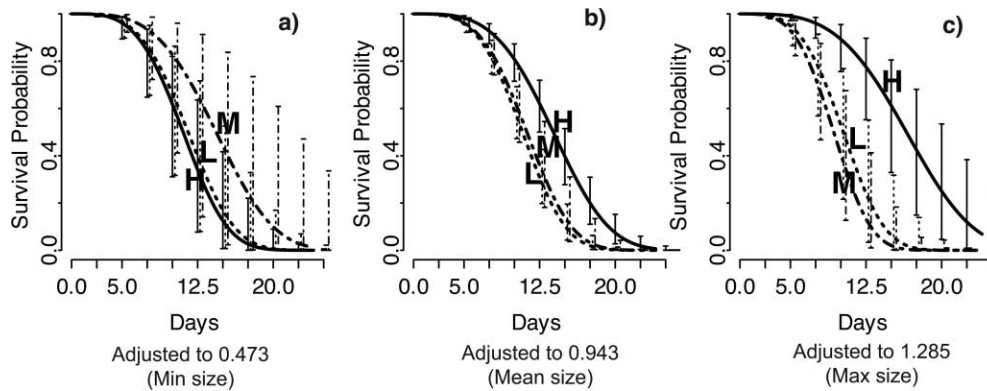
Figure 4: Food availability influences the age at death of females. Curves represent fitted survival functions from the accelerated failure time model, with bars representing 95% confidence intervals. The plots show the effect of high (H), medium (M), and low (L) adult food on the predicted survival of minimum-sized (0.483 mm; *a*), mean-sized (0.943 mm, *b*), and maximum-sized (1.285 mm, *c*) females. Although the effects of high food are most apparent in large females, the interaction between body size and food treatment was not significant ($P = .063$).

ronments (fig. 5; age at death × rearing food $F = 5.561$, df $= 1$, $P < .006$). In females reared in high- and low-food environments, variation in lifetime reproductive effort was strongly related to age at death and was slightly higher for females reared in high-food environments irrespective of adult food (fig. 5). However, in females reared in medium-food environments, variation in lifetime reproductive effort was less affected by age at death but was instead more sensitive to the adult food environment than in the other treatments (fig. 5; rearing food × adult food $F = 3.082$, df $= 4$, $P < .006$), suggesting that the interaction between rearing food and adult food may be important in determining egg-laying schedules. After rearing food and adult food were fitted, body size failed to explain any further variation in lifetime reproductive output (size $F = 0.369$, df $= 1$, $P = .545$). Consequently, lifetime reproductive output was greatest in large females that had access to high food and

lived for a long time (fig. 5, *left*). The lowest lifetime reproductive output was associated with small females that experienced low adult food (fig. 5, *right*).

Experiment 2: Pheromone Cues, Offspring Provisioning Strategy, and Age at Death

In experiment 2, as in experiment 1, the size of eggs females laid increased with age in both high- and low-food environments (LRT age $= 57.79$, df $= 1$, $P < .0001$), whereas the number of eggs that females laid decreased in both high- and low-food environments (LRT age $= 32.3$, df $= 1$, $P < .0001$). We found no effect of the pheromone cue on either the size of eggs that females laid throughout their lives (LRT treatment $= 0.002$, df $= 1$, $P = .97$) or the number of eggs that females laid throughout their lives (LRT treatment $= 0.8$, df $= 1$, $P = .38$). Females with access to more food lived longer (fig. 6; LRT
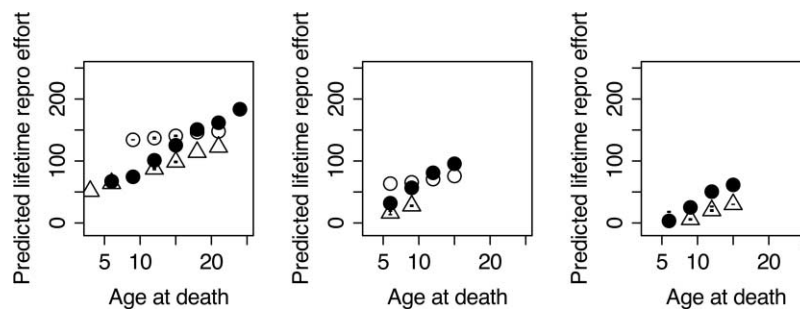

Figure 5: Predicted relationship between age at death and lifetime reproductive effort for females in either high, medium, or a low adult food environment (*left to right*). Each point represents the mean ± SE predictions of the best-fitting general linear model (see "Results"). The symbols refer to females reared in high-food (*filled circles*), medium-food (*open circles*), and low-food (*triangles*) conditions.
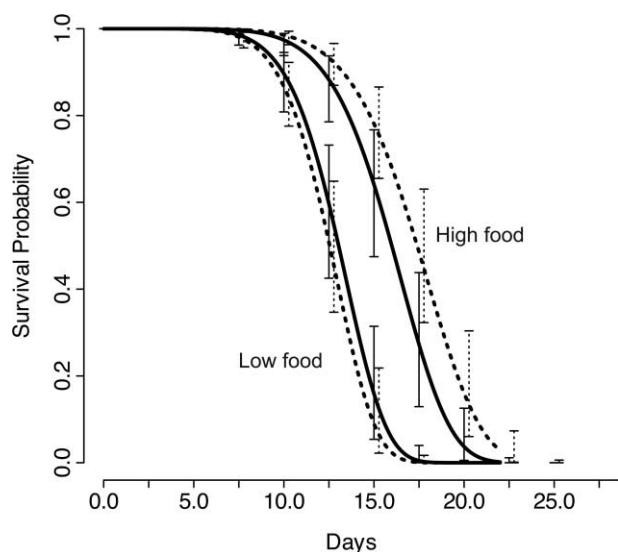
Figure 6: Fitted survival functions from the accelerated failure time model, examining the effects of adult food and exposure to colony pheromone (*dotted lines*) and nonexposure to colony pheromone (*solid lines*) on female survival. The bars represent 95% confidence intervals. Low adult food reduces female survival; however, we found no difference in the survival curves of females exposed to colony pheromone and those reared in isolation.

food $= 39.04$, df $= 1$, $P < .0001$); however, there was no difference in the age at death of females exposed to population pheromone cues and those that were isolated (fig. 6; LRT treatment $= 0.53$, df $= 1$, $P = .47$).

Discussion

A female's offspring provisioning strategy can be defined as the number and size of eggs that she lays during the course of her lifetime. In general, larger females laid larger eggs than smaller females. This finding is typical among arthropods (Bernardo 1996; Fox and Czesak 2000) and is most probably the result of morphological or physiological constraints that generate genetic or phenotypic correlations between female size and progeny size (Fox and Czesak 2000). However, our results also clearly demonstrate a dynamic shift in the way that mothers provision their offspring as they get older, changing from an emphasis on egg number in young females to larger egg size in older females (fig. 2). As a result, the covariation between egg size and egg number changed as females aged (fig. 3).

Despite the fact that theoretical models often predict an optimum egg size or clutch size (Smith and Fretwell 1974; Brockelman 1975; Parker and Begon 1986; McGinley et al. 1987; Wilson and Lessells 1994), age-related changes

in egg size and fecundity are frequently documented in a range of different systems (Bernardo 1996; Fox and Czesak 2000). Hypotheses put forward to explain age-related changes in offspring provisioning traits often focus on constraints or adaptive changes in reproductive effort over the course of a lifetime. For instance, the terminal-investment hypothesis predicts that reproductive effort should increase as females get older and the value of future reproduction begins to decline (Williams 1966*a*, 1966*b*; Gadgil and Bossert 1970; Pianka and Parker 1975). In contrast, theories of senescence generally predict that reproductive effort will decline with age as maintenance costs increase and resources become depleted (Williams 1957; Rose 1991). Finally, the Winkler and Wallin hypothesis predicts that reproductive effort should increase when per capita investment in offspring is low, that is, when offspring are cheap (Winkler and Wallin 1987). We found that in both experiment 1 and experiment 2, fecundity decreased with age but the size of eggs females laid increased with age (fig. 2). Assuming that 50%–60% drops in fecundity with age are a more important determinant of reproductive effort than the typically 10%–15% change in the size of individual eggs over the course of a female's lifetime (fig. 2), overall reproductive effort declined with age in *Sancassania berlesei*, the opposite pattern to that predicted by the terminal–reproductive investment hypothesis. The reduction in reproductive effort with age is also unlikely to be the result of senescence because this would predict a decline in the size of eggs that females laid as they got older. An alternative explanation for our findings is that reproductive effort declines with age in *S. berlesei* because there is strong selection for early reproductive effort in this system (Charlesworth and Leon 1976; Charlesworth 1994). This is likely in populations that frequently experience high density-dependent mortality and/ or frequent opportunities for rapid population growth, both of which are likely in opportunistic species, such as *S. berlesei*, that have evolved a life history that specializes in exploiting patchily distributed resources of high energy content, such as carcasses and piles of dung (Houck and O'Connor 1991).

Our results are not inconsistent with the Winkler and Wallin (1987) hypothesis, given that the decline in reproductive effort in older female *S. berlesei* coincided with an increase in the per capita investment in each egg (fig. 2). However, our findings also provide general support for models that predict that increasing levels of sib competition select for better-provisioned offspring (Parker and Begon 1986). Bridges and Heppell (1996) found the same pattern of lifetime offspring provisioning (increasing per offspring investment and decreasing fecundity) in the opportunistic polychaete worm *Streblospio benedicti*. Using a matrix model, they demonstrated that a switch from fe-

cundity to increased per-offspring investment could be adaptive if increasing investment in each offspring increased its probability of survival. In *S. berlesei*, hatching from a larger egg in low-food environments increases recruitment, whereas egg size has little effect on recruitment in high-food environments (Plaistow et al. 2006), supporting the idea that increasing egg size with age may be an adaptive strategy designed to maximize the total number of surviving offspring. If this is true, mothers might also be expected to alter their reproductive schedule in different food environments.

Life-history theory predicts an increase in early reproductive effort if an individual's own probability of surviving is reduced (Fisher 1930; Williams 1966*a*, 1966*b*; Schaffer 1974, 1979; Pianka and Parker 1975). However, mothers might also increase their investment in early reproduction, at the expense of their own survival, if staying alive longer decreases the probability that their own offspring recruit (Evans et al. 1995; Travis 2004; Dytham and Travis 2006). Clearly, this will depend on the food levels that females and their offspring have access to. In this study, we found that adult food levels were the major determinant of maternal survival patterns (figs. 4, 6); however, it is difficult to determine whether the significantly reduced maternal survival in low-food conditions is adaptive or just a consequence of having no food. Female *S. berlesei* in high-food conditions (low density) maximized the number of eggs they laid at the beginning of their lives (see fig. 2) and lived for a long time (figs. 4, 6). In this case, the offspring that they generate probably represent a significant part of the competitive environment. Moreover, the competitive asymmetry between early and late offspring will be greater, increasing the need to protect later offspring. In contrast, in low-food conditions (high density), females were able to lay only a few eggs and died earlier (figs. 4, 6). Consequently, there was less need to compensate for sibling competition. We suspect that the reason that young females in low-food environments have a positive relationship between egg size and egg number, rather than the negative one seen in medium- and high-food environments, is that in low-food environments, constraints on egg production may be more important than variation in patterns of resource allocation. This idea is supported by the fact that females that laid the smallest number of eggs were LL-treatment females, which grew up in low-food conditions and also laid eggs in low-food conditions (see fig. 2, *right*). Our finding that rearing food also influenced the relative effect of the adult food environment and age at death on lifetime reproductive success (fig. 5) suggests that the interaction between rearing food and adult food may be important in determining egg provisioning schedules. Such sensory cuing of oogenesis and adaptive shifts in ovarian dynamics may be quite common in insects that have to cope with variable environments (Papaj 2000; Jervis et al. 2001).

The offspring provisioning strategy that has evolved in mites is one in which females reduce competition among siblings in high-food environments in order to maximize their total number of surviving offspring. This is the opposite pattern to that seen in many brood-reducing species of birds, in which mothers increase sibling competition in poor food environments (hatching asynchrony) in order to ensure that at least one offspring survives (Mock and Parker 1997). We found no effect of exposure to colony pheromone on any aspect of a female's lifetime offspring provisioning strategy. This could simply be because females use cues other than pheromones to assess levels of competition. Studies of several other species have shown that females change the size or the number of eggs that they lay when females encounter crowded environments (Kawecki 1995; Creighton 2005). If the resource patches that mites normally occupy vary in size, such that large patches can support large populations of mites, then clearly per capita food availability will be a better predictor of the competitive environment than simply detecting the presence of other mites. This is not necessarily true for males, however, because the presence of any other males will greatly decrease the utility of developing as a fighter in the hope of establishing a harem (Radwan 1993). While it is generally assumed that the fighting strategy seen in several mite species has evolved in response to the risk of sperm competition (Radwan 1993; Radwan et al. 2002), males that kill other males present will also increase the per capita resources available to each female and may therefore increase their fecundities and, subsequently, their own fitness.

In conclusion, we have shown that in soil mites *S. berlesei*, offspring provisioning strategies are complex and dependent on an interaction between larvae-derived resources that determine body size and the resource availability that females have during egg laying. The pattern of provisioning is dynamic, changing from an emphasis on egg number in young females to egg size in older females. As a result, the slope of the relationship between egg number and egg size is age dependent and may explain why other studies that have investigated the egg number–egg size trade-off without any consideration of female age often report mixed results (Bernardo 1996). Our results suggest that selection operates on an integrated suite of traits that together define the optimal offspring provisioning strategy for any given environment. The adaptive significance of maternal effects may be missed when studies consider only a snapshot of a female's offspring provisioning strategy or when components of it are studied in isolation.

Acknowledgments

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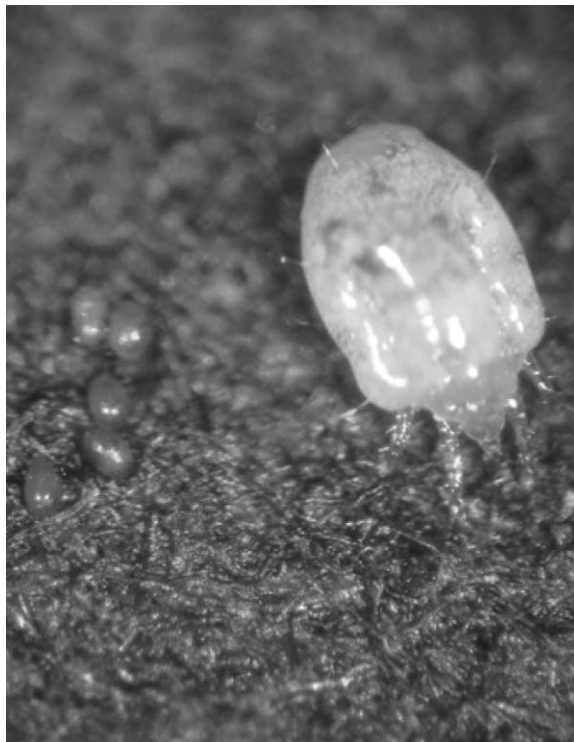
A female *Sancassania berlesei* next to five eggs she has laid. Photograph by T. Benton.