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Maternal investment in a spider with suicidal maternal care, *Stegodyphus lineatus* (Araneae, Eresidae)

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Providing parental care is costly for the parent, but generally beneficial for the young whose survival, growth and reproductive value can be increased. Selection should strongly favour an optimal distribution of parental resources, depending on the relationship between the costs and benefits for parents and their offspring. Parental care is characterized by trade offs in investment, for example between egg size and number of young or providing resources at the egg stage versus the post-hatching stage. Females of the spider *Stegodyphus lineatus* (Eresidae) produce a single small brood with small eggs and provide the young with regurgitated fluid and later, with their body contents via matriphagy. We asked whether females adjust the investment of resources differentially into eggs, regurgitation feeding and matriphagy, and how maternal investment affects the size of the young at dispersal. We followed the growth of young of broods in the lab and in the field and manipulated brood size in order to determine the pattern of resource allocation. We found that brood size was positively correlated with body mass: larger females had larger broods. Females provided 95% of their body mass to the young, allocating more resources to regurgitation than to matriphagy. Females provided regurgitated food to the young according to the brood size, providing less food when the brood was reduced. Maternal resources had a large influence on offspring mass at dispersal, which is likely to affect their future fitness. The study shows the importance of the female's body mass and her resource allocation decisions for her reproductive outcome.

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Providing parental care is costly for the parent because it limits investment in future reproduction, but it is generally beneficial for the individual young whose survival, growth and reproductive value can be increased (Clutton-Brock 1991, Fox and Czesak 2000). Selection should strongly favour an optimal distribution of parental resources, depending on the relation between costs and benefits for parents and their offspring.

Reproductive resources can be allocated to the young in different ways, and parents will be selected to distribute their resources optimally between their offspring and between different reproductive stages. When oviparous females provide post-hatching care, maternal resources can be provided both at the egg stage and to the young directly. Assuming a fixed amount of resources assigned to reproduction, there is a trade off between the number and size of the progeny (Fox and Czesak 2000): increased investment into larger eggs will be followed by a reduction in egg number. Furthermore, while allocating resources mainly to the egg stage will produce large, yolk-rich eggs, retention of resources for post-hatching care may prolong the development of the

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young and provide the female with more control over the distribution of food. Hence, there are three levels of questions regarding the pattern of resource allocation to offspring: the first level addresses the classical trade off between offspring size and offspring number (Smith and Fretwell 1974, Sterns 1992), the second level addresses the investment into eggs versus directly to the young, and the third addresses the allocation of resources directly to the young at different stages of development.

In many oviparous species parental care results in an increased investment in egg size (Shine 1978, Thresher 1984, Grahame and Branch 1985, Nussbaum 1985, Sargent et al. 1987). Investment in young via post-hatching maternal care is relatively uncommon among invertebrates (Clutton-Brock 1991), but is evident in several spider families. Maternal care in spiders includes provisioning the young with prey (Foelix 1996) or with trophic eggs (Evans et al. 1995), regurgitating digested material (Kullmann and Zimmermann 1975) and matriphagy i.e. consumption of the mother by her young (Seibt and Wickler 1987). In this study, we investigated maternal resource allocation decisions in a spider with extended post-hatching maternal care.

Semelparous species are especially suitable to investigate maternal allocation patterns because the trade off between current and future reproduction is removed when females invest all their resources into a single reproduction event (Tallamy and Brown 1999). Matriphagy is an extreme form of semelparous maternal care. In the semelparous spider *Stegodyphus lineatus* (Eresidae), females produce a single small clutch with small eggs, feed their young by regurgitation and are finally consumed entirely by their young (Schneider 1996a). Thus, a female *S. lineatus* invests all her resources in a single reproductive event and her resource allocation decisions are all within one brood. These decisions include: a) how much to invest in each egg (egg size), b) how many eggs to lay, c) what proportion of her resources to provide the young at regurgitation, and d) how much to leave for the young at matriphagy. Egg size will directly affect the number of eggs produced, and the proportion of maternal resources provided at regurgitation will clearly affect the amount of resources left for the young at matriphagy. The allocation of food to the young via regurgitation feeding or matriphagy may be a maternal decision, but could also be determined by the young.

A large proportion of the resources an offspring needs for its development are obtained in the juvenile stage (Bernardo 1996). The allocation of resources between regurgitation and matriphagy may be important to the development of the young if there is a difference in food quality between these stages. The regurgitated material in *Stegodyphus pacificus* was suggested by Nawabi (1974) to consist of a mixture of predigested food and the female's intestinal tissues, and may also contain maternal fat tissue, which provided additional energy. In addition, providing already digested material in regurgitation does not require investment of the young in venom and enzymatic fluids and thus may be of higher value to the young than the mother's tissues consumed at matriphagy.

Young that obtain a large amount of resources from the mother are more likely to grow to large adults and thus have a higher fitness. Offspring size was positively correlated with survival and feeding success (a measure of offspring fitness) in the wolf spider *Hogna helluo* (Lycosidae) (Walker et al. 2003) and in *S. lineatus*, the size of the young influenced both their survival (Schneider 1992) and reproductive value (Ward and Lubin 1993). We expect that the amount and allocation of resources in maternal care will have a direct influence on the body mass of young at dispersal and consequently on their fitness.

Our objectives were to examine how the female allocates her resources to the different components of reproduction and how her decisions affect the young. We asked the following questions: 1) how are the maternal resources divided a) between egg size and number of eggs? b) between eggs and post-hatching feeding, and c) between the stages of regurgitation and matriphagy? 2) What is the effect of brood size on maternal investment decisions? And 3) how does variation in resource allocation affect offspring size at dispersal?

We followed the growth of young in field nests and in nests kept in the laboratory, and determined the patterns of maternal resource allocation. We then conducted a laboratory experiment whereby brood sizes were reduced or enlarged to determine the impact of brood size on resource allocation and on growth of young during maternal care. Varying post-hatching brood size has the effect of changing the amount of resources available from the mother relative to her brood mass. As the mother provides most of her resources to the young during regurgitation and matriphagy (Schneider 1996a), we predicted that (1) the amount of maternal resources provided during these two stages will strongly affect the size of the young at dispersal, and (2) young in reduced broods will receive more food from their mother and thus have a larger body mass at dispersal than young in increased broods.

Methods

Life history

Stegodyphus lineatus is an annual and semelparous species, which builds its nests and webs on trees and bushes in a desert environment (mainly along seasonally dry watercourses). Mating in this species occurs in the spring, and after two weeks the female produces a single egg sac, which contains about 90 eggs (Schneider 1995, per. obs.). The entire egg sac constitutes only 2–3% of the female's initial body mass (Schneider 1996a). The female will produce a second egg sac only if the first was not viable (per. obs.), if it was taken by a predator, or removed by an infanticidal male (Schneider and Lubin 1997).

Approximately 30 days after egg laying, the female opens the egg sac and releases the hatched spiderlings. During a period of around two weeks after hatching the female does not catch prey, but feeds the young with regurgitated material, and finally provides them with her body as food (matriphagy). At matriphagy, the spiderlings climb on the female's body and consume her, extracting her body fluids within two to three hours and leaving only the exoskeleton (per. obs.). The occurrence of matriphagy is inflexible and is likely to be a conservative trait in this genus (Schneider 2002, but see below). The spiderlings stay in the maternal nest for two weeks or more after matriphagy, and then disperse gradually (Aviram 2000). The female does not provide prey items to the young and the young do not catch prey by themselves before matriphagy. Only after matriphagy the young construct small capture webs while still living communally in the maternal nest (per. obs.) and feed on small prey items (Aviram 2000).

Laboratory and field observations

During April–May 2001, we collected nests of adult females with egg sacs near Lehavim, in the northern Negev, Israel. The spiders were kept in mesh boxes outside in natural conditions at the Jacob Blaustein Institute for Desert Research in Sede Boqer (about 70 km south of Lehavim). The females were provided with 1–2 grasshoppers (*Locusta* sp.) or flour beetles (*Tenebrio molitor*) per week until the spiderlings hatched. We recorded the hatching and matriphagy dates and the date at which about 10% of the brood had dispersed from the nest.

Since dispersal is not a discrete process but is attained gradually, we chose a time early in the dispersal stage in order to be able to compare between different broods. Spiderlings after matriphagy were fed with cricket nymphs (*Acheta domestica*) until they dispersed from the nest.

At each life history stage (two days after hatching, one day after matriphagy, at dispersal, and two weeks post-dispersal) we weighed a sample of spiderlings to 0.01 mg accuracy and counted the number of individuals in the nest. Eggs and spiderlings immediately after hatching were too delicate to weigh. Therefore, we used spiderling body mass two days after hatching as an estimate of the female's resource investment in each egg. We refer to this measure as 'average mass at hatching'. Although the exact mass at hatching is likely to be slightly overestimated by this method, this procedure is not unusual (Toyama 2003), and allowed us to collect the data without harming the brood.

In addition, we measured the female's prosoma width and her mass two days after the spiderlings hatched, and weighed her remains after matriphagy to determine the total maternal investment in the young. Prosoma width does not change after the last molt and is a measure of size independent of body condition. A body condition index was calculated using the residuals of female body mass regressed against body size (prosoma width; Lubin et al. 1991). Both size and condition could affect the female's allocation decisions. We collected the egg sac from each nest and counted the number of unhatched eggs and dead first-instar spiderlings inside to obtain total clutch size and hatching success. Similar measurements were taken for a sample of females and their young from nests taken from the field (near Lehavim in the northern Negev), which we returned to the field after each measurement. Throughout, we use brood size to indicate the number of young in the nest.

Brood-size manipulation experiment

In May 2002, we collected females with egg sacs, near Tel Arad, in the north-eastern Negev desert. The spiders were kept in the laboratory at a temperature of 26°C and ambient light regime. Females were not fed during the month they were guarding the egg sac. We tested whether brood size affected the mother's decisions regarding allocation of resources to regurgitation and matriphagy.

The experiment included 3 treatments: A) reduced brood size treatment ($n = 20$), B) increased brood size treatment ($n = 10$) and C) control (brood size was not manipulated) ($n = 10$). In treatment A, brood size was reduced to 5 spiderlings per brood two days after hatching. The young removed were used to increase broods in treatment B by 50% of the original brood size. Spiderlings were supplemented to broods containing young hatched on the same day, so that there was no age difference between the spiderlings within the increased broods. Females in increased broods treated the additional young as their own. Spiderling mass did not vary substantially within increased broods at the end of the experiment, suggesting that there was no kin discrimination.

We measured prosoma width, recorded the hatching date, counted the number of young and weighed the female and her brood two days after hatching (before brood manipulation). We took the same measurements 12 days after hatching to obtain the amount of resources invested in the young during the regurgitation stage, and again after matriphagy to obtain the amount of resource investment in matriphagy. Previous experiments showed that the earliest time that matriphagy occurred was 12 days after hatching (unpubl.). If we took measurements at a later time, we would risk missing the end of regurgitation. Since matriphagy did not occur in the reduced brood treatment before the experiment ended, the investment in matriphagy was calculated only for the increased and control broods. The above measurements were also taken at dispersal, i.e. when 10% of the brood dispersed, to obtain the affect of the brood manipulation on the young.

Statistical analyses

We used regression analysis to determine the relationships between brood size (i.e. number of young) and mass of the young at different stages and the body size, mass and condition of the mother. We compared the treatments in the brood-size manipulation experiment with ANOVA and Bonferroni-adjusted post hoc comparisons. When necessary, log or arcsine transformations were performed to normalize the data and homogeneity was tested using O'Brien's test of equal variances. Analyses were performed with Systat 9.0 (Wilkinson 1999), except the homogeneity test, which was performed with JMPIN4 for PC (Sall et al. 2001).

Results

Clutch size and size of young

Average spiderling mass at hatching (a proxy measure of egg size) did not vary with clutch size at hatching (2001: $r^2 = 0.05$, $n = 29$, $P = 0.24$). Thus egg size and the number of eggs were determined independently. Hatching success was not influenced by female size (prosoma width; Table 1). In both years, the mother's body size did not influence brood size or average spiderling body mass at hatching (Table 1, 2). Female body mass and condition measured at hatching of the young did not explain average spiderling mass at hatching in both years (Table 1, 2), but did explain almost 30% of the variation in the number of young in 2002 (Table 2).

Maternal allocation of resources after hatching

There was no significant difference at any stage in mass of the young in the nests taken from the field and those raised in captivity (Fig. 1; two-way ANOVA; treatment: $F_{1,50} = 0.002$, $P = 0.968$; stage: $F_{2,50} = 61.8$, $P < 0.001$). Spiderling mass increased markedly after matriphagy, and was maintained until dispersal from the maternal nest (Fig. 1).

Spiderling mass after regurgitation and matriphagy, a measure of total female investment in care of young, was positively correlated with initial female mass measured when the young hatched (2001: $r = 0.633$, $n = 22$, $P = 0.002$). Female body mass explained 40.1% of the variation in the mass of young after matriphagy, using residuals of female mass on brood size to correct for variation in brood size.

All females lost a large percentage of their body mass (92–96%) due to regurgitation and matriphagy (Fig. 2). Broods of large females obtained a significantly larger percentage of the female's body mass than did broods of smaller females (2001: $r^2 = 0.594$, $n = 19$, $P < 0.001$). This may be a simple result of scaling: mass increases to the power of 3 and the exoskeleton to the power of 2 (Price 1997), or it may be that large females actually give a higher percentage of their body mass compared to small females.

Brood size manipulations: differential resource allocation during maternal care

Neither initial female mass nor initial brood size differed between the reduced, increased and control treatments (ANOVA: female mass; $n = 40$, $P = 0.09$; brood size; $n = 40$, $P = 0.409$). In the control treatment females provided a significantly lower percentage of their body mass to the young in regurgitation (41% on average, measured at day 12 after hatching) than at matriphagy (54.4%; Fig. 3; paired t-test: $t = -2.481$, $n = 20$, $P = 0.035$). At day 12 post-hatching, there was a significant difference between the percent of mass lost by the female during regurgitation in the different treatments (ANOVA: $F_{2,35} = 97.18$, $P < 0.001$). A post hoc test revealed that females in the reduced brood size lost significantly less mass than those in both the increased and control treatments ($P < 0.001$

Table 1. Linear regression results of offspring vs female variables at hatching in 2001($n = 29$).

Dependant variable	Mean ± SE	Female prosoma width (mm) 4.1 ± 0.05			Female mass (mg) 562.7 ± 28.66			Female condition index		
		r^2	slope	P	r^2	slope	P	r^2	slope	P
Brood size	75.3 ± 4.53	0.002	3.6	0.84	0.008	7.93	0.65	0.006	−8.16	0.68
Hatchling mass (mg)	1.6 ± 0.16	0.002	0.07	0.83	0.04	0.33	0.3	0.063	0.48	0.19
Hatching success	0.82 ± 0.03	0.006	0.1	0.7						

Table 2. Linear regression results of offspring vs female variables at hatching in the 2002 brood manipulation experiment (n = 57). 2002 data include all three treatments before brood manipulation.

Dependant variable	Mean ± SE	Female prosoma width (mm) 4.13 ± 0.045			Female mass (mg) 632.8 ± 24.28			Female condition index		
		r^2	slope	P	r^2	slope	P	r^2	slope	P
Brood size	71.98 ± 4.54	0.021	14.52	0.28	0.296	66.42	< 0.001	0.287	73.37	< 0.001
Hatchling mass (mg)	0.65 ± 0.03	0.044	0.14	0.117	0.003	0.046	0.67	0.029	0.154	0.2

for both). Females in the reduced treatment provided only 13% of their body mass in regurgitation, where females in the increased brood size and control treatments provided 46.1% and 41%, respectively. The rate of regurgitation per day, calculated from female mass loss during 12 days of regurgitation was significantly lower for the reduced broods (mean ± SE; 1.07% ± 0.1), than for increased (3.84% ± 0.18) and control broods (3.41% ± 0.2; ANOVA: $F_{2,35} = 97.18$, $P < 0.001$).

At matriphagy, there was no significant difference between the percentage of mass lost by females in the increased brood (49.5%) and the control treatments (54.4%; t-test: $t = 1.402$, $n = 19$, $P = 0.179$). Females in both increased and control treatments gave their young a total of 95.5 ± 0.01% of their body mass during brood care. In the increased brood treatment, females provided 5% more in regurgitation than females in the control treatment (Fig. 3) and 5% less at matriphagy; this difference was not statistically significant.

Matriphagy occurred in all of the increased and control broods but did not occur in the reduced broods during the two weeks post-hatching period of the experiment. Matriphagy did occur later in 7 out of 20 of the reduced broods (35%). There was a significant difference in time from hatching to matriphagy between the brood manipulations treatments (ANOVA: $F_{2,24} = 14.22$, $P < 0.001$). Matriphagy occurred at a significantly later date in the reduced broods than in the control broods (mean ± SE; 52.71 ± 10.16 and 22.6 ± 1.51 days, respectively; $P < 0.001$) and earlier in the increased broods (17.8 ± 1.4 days) than in the control broods ($P = 0.039$).

Consequences of maternal care for the young

Spiderling mass after dispersal was positively influenced by initial female mass (2001: Fig. 4: $r^2 = 0.46$, $n = 25$, $P < 0.001$). Therefore, broods of large females were provided with more resources per capita than broods of small females, and the effect lasted until dispersal.

In the brood manipulation experiment, we found that average spiderling mass at dispersal was lower in the increased broods than in the control broods, although the difference was not significant (4.64 ± 0.46 and 6.7 ± 1.03 mg, respectively; t-test: $n = 20$, $P = 0.093$).

Timing of dispersal

Broods with large young dispersed later from the mother's nest than broods with small young (2001: Fig. 5; $r^2 = 0.29$, $n = 22$, $P = 0.01$). Neither the number of dispersing young nor their coefficient of variation in mass (% CV) within a brood could explain the

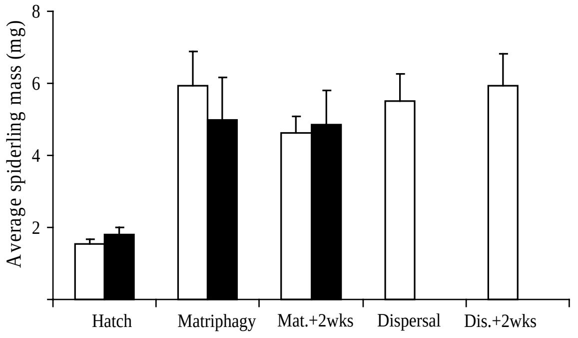

Fig. 1. Spiderling body mass (mean and SD) in captivity (white bars) and in the field (black bars) at different stages of development: two days after hatching, after matriphagy, two weeks post-matriphagy, at dispersal and two weeks after dispersal. The latter two measurements are from spiders maintained in captivity.

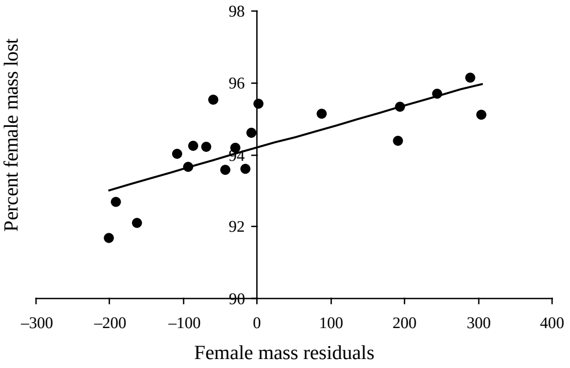

Fig. 2. Female mass loss at the end of maternal care: percent of body mass lost by the female after being consumed by her young in relation to female body mass residuals (corrected for brood size at hatching by regression) Regression: $y = 0.006x + 94.2$. ($R^2 = 0.6$, $r = 0.77$, $n = 17$, $P < 0.001$).

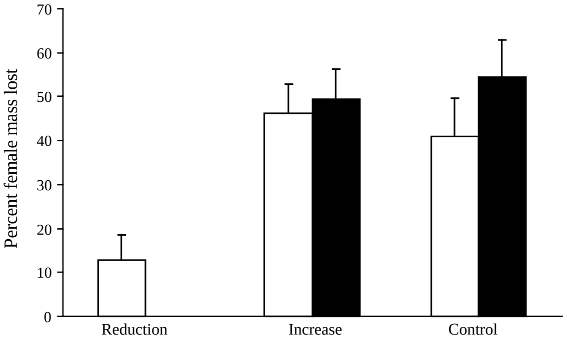

Fig. 3. Female mass loss (mean percent of initial body mass and SD) after regurgitation (white bars) and after matriphagy (black bars) in the different brood size treatments. The 5% difference in allocation between increased broods and control broods is not statistically significant.

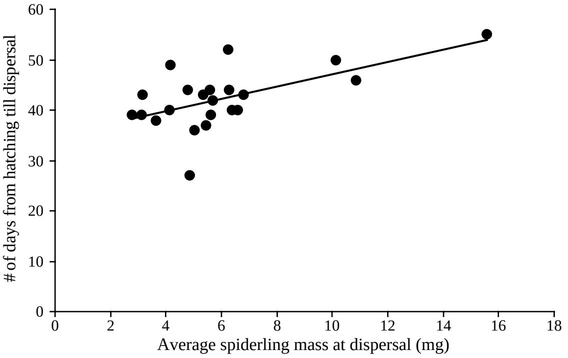

Fig. 5. Time from hatching until dispersal in relation to average spiderling mass at dispersal, 2001 data set. Regression: $y = 1.2224x + 34.927$. ($R^2 = 0.29$, $r = 0.54$, $n = 22$, $P = 0.01$).

differences in the timing of dispersal (brood size at dispersal; $n = 22$, $r^2 = 0.07$, $P = 0.235$; mass CV; $n = 22$, $r^2 = 0.129$, $P = 0.1$).

We expected that experimentally increased broods, with their smaller young, would disperse earlier than control broods, owing to increased competition for resources. Indeed, young in the control treatment dispersed 4 days later than those in the increased brood treatment (41.5 ± 0.98 and 37.6 ± 1.7, respectively; ANOVA; $n = 15$, $P = 0.063$). No young reached dispersal in the reduced brood treatment during the experiment, but 8 broods dispersed 72.25 ± 11.6 days after hatching.

Discussion

Stegodyphus lineatus females produce a single clutch containing few eggs relative to their body mass (Schneider 1996a). The size of the mother did not explain the number of eggs nor the size of eggs produced. However, brood size was positively correlated with maternal mass and condition only in one of two years, although earlier studies also show a significant correlation (Schneider 1992, 1996a). Generally, clutch size is a function of maternal body mass in spiders (Killebrew and Ford 1985, Marshall and Gittleman 1994) resulting in strong fecundity selection on increased female mass in many species. However, most spiders do not provide maternal care after egg production and in a species with extreme post-hatching care, clutch size is likely to be influenced by the female's decisions regarding the allocation of resources into eggs versus young. When selection favors retention of resources for post-hatching development of the young, then there will be a weaker correlation between clutch size and female size and mass.

In *S. lineatus*, most of the female's investment in maternal care occurs in regurgitation feeding and at matriphagy, rather than in the egg stage. By the end of the maternal care period the young consumed 95% of their mother's body mass, leaving an empty exoskeleton. In experimentally reduced broods, female mass loss per day was substantially less than in control or increased broods, and matriphagy occurred very late or not at all indicating that the few remaining young do not utilize all of their mother's resources. Matriphagy occurred relatively earlier in increased broods, suggesting increased competition for maternal resources. Thus, the amount of resources that the young received was a function of maternal condition and brood size, while offspring size at dispersal depended on the mother's mass and condition discounted by brood size.

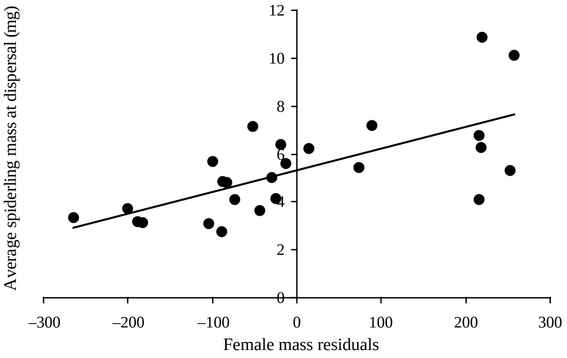

Fig. 4. Average spiderling mass per brood at dispersal in relation to initial female mass at hatching of her young. Regression: $y = 0.009x + 0.62$. ($R^2 = 0.4$, $r = 0.64$, $n = 25$, $P = 0.001$).

Clutch size and size of young

Offspring mass measured two days after hatching (our proxy measure of egg size) was not correlated with clutch size. Thus, we suggest that there is no trade off between clutch size and egg size in this species and each variable is determined separately. Offspring mass at hatching (and consequently egg size) appears to be relatively constant and independent of female size and body mass. Schneider (1996a) suggested that the high risk of parasitism for the female at the egg stage selects for small eggs, which will develop rapidly, thus shortening the period of high risk. Alternatively, egg size may be fixed phylogenetically, leaving females the possibility of varying only the clutch size. The variation in brood size was explained partly by female mass and condition, but not by female body size. Thus females in good condition invest in producing more young, rather than larger eggs. Similar results were found in the spider *Chiracanthium japonica* (Clubionidae), which also engages in terminal maternal care, where females with a large amount of reserves produced a larger number of offspring, but not larger-sized young at hatching (Toyama 2003).

Maternal care after hatching

Spiderling mass increased sharply after maternal care (observed also in another species with maternal care; *Amaurobius ferox*, Kim et al. 2000) and remained at a similar level until dispersal. This large increase in spiderling mass is due to the resources provided to the young by the female in regurgitation and matriphagy combined (92–96% of female body mass). We found that heavy females produce more young and also provided them with more food, thus obtaining both large broods and large young after matriphagy. These results are in contrast to those found for *C. japonica* in which the offspring mass after matriphagy was not related to female reserves (Toyama 2003). In contrast to *C. japonica*, *S. lineatus* shows a larger influence of the female's body mass and condition on growth of her young. Thus, fecundity selection under such strong maternal effects, may act to maximize maternal body mass or condition, rather than body size.

Partitioning of resources to regurgitation and matriphagy

Significantly fewer resources were provided during regurgitation (41% of total female mass in the control group) than during matriphagy (54%). The reason for this may be a physiological constraint on the ability to mobilize food for regurgitation. Females may be limited by the amount of partly digested prey and intestinal tissues that they are able to liquefy and secrete to the young. There should be an advantage in providing more regurgitated fluid over leaving resources for matriphagy because of its possible higher energetic and higher nutritional value to the young. Nawabi (1974) suggested that the regurgitated fluid includes both dissolved tissue and glycogen, which would provide both energy and nutrients to the young.

The mass loss through regurgitation was lower for females with reduced broods, but females with increased broods did not significantly increase the food provided to the young over the control group. Assuming a constant rate of regurgitation until matriphagy, the rate of regurgitation per day was lower in the reduced broods (1.07%) than in the increased (3.8%) or control broods (3.4%). This suggests that although the female is able to regurgitate slightly more food when the brood is enlarged, there is little flexibility in her ability to deliver more resources to an enlarged brood. However, the 5% increase in the percentage of food provided at regurgitation to enlarged broods may have been enough to compensate for the increase in brood size, and to enable the young to disperse at a body mass similar to that of control broods.

The delivery of regurgitated fluid may be controlled either by the mother or by the young. While the mother may prefer to reserve some resources for a replacement clutch in case the single clutch is lost, each offspring is expected to attempt to maximize the amount of food it can get from the female. In adjusting the amount of food regurgitated, females may assess brood size through (a) encounters with the young, or (b) the feeding rate of the young. Alternatively, (c) the young may engage in begging behaviour and the female provides food in response to this behaviour. A behavior where the young push their heads against the female's mouthparts was observed in the burying beetle, *Nicrophorus vespilloides* (Smiseth and Moore 2002) and interpreted as begging. In the spider *Coelotes terrestris* (Agelenidae), the young solicit food from the mother by stroking the female with their forelegs, a behaviour that may be a form of begging (Gundermann et al. 1988). According to Trivers (1974), begging evolved as a strategy by which the offspring attempt to extract more resources than the parents are willing to provide. Even in a semelparous species, such a conflict is possible if there is some advantage to females to regulate the delivery rate of food or to delay matriphagy. By regulating the amount of food given to the young in each bout of regurgitation and by spreading the bouts over time (per. obs.), a female may increase the probability that all the young will receive food. This in turn may reduce the variation in size among the young. The resulting similarity in competitive ability might explain the low cannibalism rate found in juveniles of *S. lineatus* (Bilde and Lubin 2001).

The timing of matriphagy seems to be influenced by both the female and her young (also shown in Schneider 2002). In *A. ferox*, matriphagy occurs following web vibrations signals between the female and the young (Kim and Horel 1998). No such signaling has been seen in *S. lineatus* and matriphagy may begin when the female is no longer able to provide more regurgitated fluid.

In the spider *C. japonica*, matriphagy is not always necessary in order for spiderlings to initiate dispersal, but sufficient food provisioning is essential (Toyama 2003). *S. lineatus* young that were separated from their mother two or five days after hatching and provided with ad lib fruit flies did not survive (unpubl.). Thus, regurgitation feeding is essential for the development of the young. Furthermore, young that did not consume their mother, but were provided with regurgitation, were able to disperse. However, they dispersed at a much lower body mass (unpubl.), lowering their chances of survival.

Consequences of maternal care for the young

We showed a four-fold increase in mass of the young during maternal care. A previous study of *S. lineatus* young showed that the spiderlings gain even up to 10–20 times their hatching mass (Schneider 1992). The resources the young receive after hatching may have a large influence on their development and growth (Vollrath 1987). The resources provided in regurgitation and matriphagy enable the young to disperse at a larger body size, which will improve their chances of survival over winter (Schneider 1996b). Larger young are more competitive when in groups (Schneider 1995) and after dispersal they will construct larger webs and thus catch more prey (Ward and Lubin 1993). They may mature earlier and thus have higher reproductive value as adults (Schneider 1996a).

Broods with large spiderlings dispersed later than broods of smaller spiderlings. In the experiment, the increased broods with small young dispersed before the control broods. As the spiderlings' energetic needs increase with their development, the food inside the nest become scarcer. This problem may be more intense for small spiderlings with limited body reserves, where a short period of starvation may be lethal. Insufficient food and competition, including aggressive interactions and cannibalism may all be responsible for the early dispersal observed in the broods containing small spiderlings.

In this study we have shown strong maternal effects, mediated by regurgitation feeding and matriphagy, on the size of the young at dispersal. Maternal body mass and condition have the strongest effect on the development of the young, but this relationship can be influenced also by brood size. We suggest that the nutritional quality of the food provided to the young at different stages could play a role in survival and growth of the young during maternal care. However, this remains to be investigated.

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