

Maternal Body-mass Transfer to Offspring in the Matriphagous Spider, *Amaurobius ferox* (Amaurobiidae)

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ABSTRACT: The optimal strategy for semelparous females may involve adjustments in the relative investment in two fitness components, the number of offspring and the post-hatching investment per capita. To determine the pattern of maternal resource allocation to offspring in the matriphagous spider, *Amaurobius ferox* (Amaurobiidae), I investigated the relationship between maternal body-mass and the number of offspring, and quantified the transfer of maternal body-mass to the offspring via different forms of maternal provisioning (trophic egg-laying and matriphagy). There was a positive relationship between female body-mass and the number of offspring. However, *Amaurobius* mothers did not produce more trophic eggs when they had larger broods. Rather, spiderlings in larger *A. ferox* broods consumed larger quantities of maternal body-mass via matriphagy. Mothers transferred $28.8 \pm 6.5\%$ of their body-mass to the spiderlings via trophic egg-laying, and an estimated $39.0 \pm 12.5\%$ of their body-mass was transferred to the spiderlings via matriphagy.

Key words: *Amaurobius*, Brood size, Maternal body-mass, Maternal food, Matriphagy

INTRODUCTION

Postzygotic maternal investment involves a trade-off between current and future reproduction, because investment in current offspring involves costs in terms of future offspring numbers or fitness (Trivers 1972, Clutton-Brock 1991) for animals which have the potential to experience more than one opportunity for reproduction (e. g. iteroparity *sensu*, Fritz et al. 1982). For semelparous species that reproduce only once in their lifetimes, however, no trade-off between current and future reproduction constrains them from maximizing maternal care in response to environmental challenges (Tallamy and Brown 1999), and individuals may allocate all of their resources to maximize the fitness of the current offspring.

Females providing post-hatching maternal care can allocate resources to their offspring in various ways, and parents will be selected to distribute their resources optimally among their offspring and among the different developmental stages of the offspring (Clutton-Brock 1991, Salomon et al. 2005). The optimal strategy for semelparous females with limited reproductive resources is to allocate their reproductive resources between two fitness components, offspring number and post-hatching investment per capita, so as to maximize their own fitness returns (Smith and Fretwell 1974, Toyama 2003).

Matriphagy (maternal feeding of the offspring using the mother's body as food), an extreme form of semelparous maternal care, occurs

in the black lace-weaver spider, *Amaurobius ferox* (Amaurobiidae), which displays an unusual set of maternal behaviors. The mothers provision their offspring twice: first with a batch of trophic eggs which is immediately eaten by the spiderlings (Kim and Roland 2000), and later via matriphagy (Kim and Horel 1998). The trophic eggs and matriphagy improve development and survival of the offspring (Kim and Roland 2000, Kim et al. 2000). The mothers are physiologically capable of producing a second clutch, but experiments show that their net reproductive output, calculated as the number of surviving midinstar juveniles, is maximized by matriphagy versus the alternative strategy of abandoning the offspring early in order to lay a second clutch (Kim et al. 2000). *A. ferox* females do not provide prey items to their spiderlings and the spiderlings do not capture prey by themselves before matriphagy (Kim et al. 2005). Therefore prey availability seems not directly affect the fitness of the offspring during the maternal period after emergence of the spiderlings from egg sac (Kim 2009) as it does in species that provide food for their young by capturing prey and carrying it into their nests, such as *Cælotes terrestris* (Amaurobiidae; Gundermann et al. 1988), *Theridion grillator* (Theridiidae; Gillespie 1990), *Anelosimus crassipes* (Theridiidae; Ito and Shinka 1993), and *Scytodes* sp. (Scytodidae; Li et al. 1999).

This study focuses on the transfer of maternal body-mass to the offspring in *A. ferox*. Where the benefits of parental care are depreciable, total parental expenditure may increase with brood size (Lazarus and Inglis 1986, Salomon et al. 2005, but see Toyama 2003).

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A. ferox, however, should face a trade-off between postzygotic maternal expenditure per offspring and brood size, because offspring development and survival depend on a limited maternal resource. A small brood could receive a good deal of maternal food per capita, whereas a very large brood will receive little maternal food per capita. I investigated the relationship between maternal body-mass and its clutch size and the allocation of maternal body-mass to the spiderlings via food provisioning in the forms of trophic eggs and matrophagy.

MATERIALS AND METHODS

Study Animal

Amaurobius ferox Walckenaer (Amaurobiidae) is a cribellate spider of dark (brownish black) color and is commonly found in shaded places in Europe (Cloudsley-Thompson 1955, Bristowe 1958). This species is relatively large compared with other spiders, and females are slightly larger than males (total body length: 8.5–14 mm vs. 8–12.5 mm; body mass: 140–320 mg vs. 80–160 mg; Cloudsley-Thompson 1955, Lemasle 1977).

A. ferox reproduces in late spring and early summer (Tahiri et al. 1989), and the reproductive activities of *A. ferox* include maternal caring behaviors performed over a fairly constant time interval after emergence of spiderlings from egg sac (Kim and Horel 1998, Kim and Roland 2000). The mother cares for the offspring for a period of about four weeks, which includes the following events: 1) a three-week incubation period during which the mother stays in close proximity to her egg sac; 2) the emergence of 60–130 spiderlings from the egg sac at the end of incubation; 3) the laying of trophic eggs, which are immediately devoured by the spiderlings one or two days after emergence (Kim and Roland 2000); 4) molting of the spiderlings three to four days later (Kim 2001); and finally 5) cannibalization of the mother by her offspring one or two days after the offspring molt (Kim and Horel 1998). In this species the mothers are always devoured by their offspring (Kim et al. 2000). After their mother's death the brood remains in their natal nest for three to four weeks until dispersal (Kim 2000).

Collection and Rearing

Inseminated females were collected from early May to early June, before the egg-laying period, from under fallen stones and in ruined walls in the forested area of Nancy, France (Northeast France, N48° 41', E6° 13', elevation: 217 m, annual temperature: 9.6 ± 6.3 °C, annual precipitation: 74 cm). Insemination was verified by the presence of a mating plug (Suhm et al. 1996).

After collection, females were transferred to a closed room lighted by fluorescent tubes (approx. 100 lux, 12L/12D) and main-

tained at a temperature of 20 ± 2 °C. Each female was placed in an individual glass terrarium (L: 200; W: 120; H: 200 mm) partly filled with a mixture of sand and peat (Tahiri et al. 1989), and the terrarium was humidified twice a week. The females received three 20 ± 2 mg cricket nymphs every three days as food, and this number of crickets was fulfilled in situation of shortage. Laboratory experiments were conducted at the Laboratoire de Biologie et Physiologie du Comportement, Université Henri Poincaré-Nancy 1, France.

Female Body-mass vs. Clutch Size

I measured the body mass of thirty females every five days before egg sac construction and used the final measurement as the estimate of female body-mass prior to egg-laying. Thus, 'the female body-mass before egg-laying' indicates the body mass one to five days prior to egg-laying. After the spiderlings' emergence from the egg sac, I counted the number of spiderlings that emerged in each clutch.

Investments of Maternal Body-mass

To investigate the relationship between the allocation of maternal body-mass and brood size (the number of spiderlings within a brood), I examined eleven broods throughout the maternal period after emergence of the spiderlings.

I counted the number of spiderlings at the emergence. Mortality of the spiderlings from emergence to matrophagy is close to zero (Kim and Roland 2000). Therefore, I did not re-count the spiderlings in the broods during this period. I measured the spiderlings' body-mass on the day after trophic egg consumption, and on the days before and after matrophagy. As the maternal provisioning occurs over a quite constant time interval in this species (Kim and Horel 1998, Kim and Roland 2000), the days of trophic egg-laying and matrophagy could be predicted to within one day: the mother provides her offspring with trophic eggs on the first day after the end of the spiderlings' emergence. The spiderlings molt 3–4 days later and then matrophagy occurs 1–2 days after this first post-emergence molt. To minimize disturbance to the brood, I measured the body mass of samples of five randomly-chosen spiderlings per brood for each measurement.

I measured the body mass of the mothers at the end of emergence, which corresponded to the day before trophic egg-laying, on the day after trophic egg-laying, and on the day before matrophagy. The proportion of maternal body-mass invested in the offspring in the form of trophic eggs was estimated as the difference between maternal body-mass before and after trophic egg-laying. The nest of *A. ferox* is made of cribellate silk, a material known for its adhesive properties (Ward and Lubin 1993, Opell 1994), which makes it very

difficult to collect every remaining fragment of the maternal carcass after matrophagy. Therefore, I estimated the maternal body-mass consumed in matrophagy from the difference between the body mass of the spiderlings before and after matrophagy. The total mass of a brood was calculated as the mean of spiderling's body-mass measured in the five randomly-selected individuals from that brood multiplied by the number of spiderlings in the brood. To calculate the proportion of maternal body-mass consumed in matrophagy, the difference in total brood mass was divided by the maternal body-mass measured on the day before matrophagy.

Statistical Analysis

I analyzed the data using linear regression analysis using Stat-View (version 5.0; SAS Institute 1999). To determine the relationship between the female's body-mass and its clutch size (the number of spiderlings), the female's body-mass was designated as the independent variable and the clutch size as the independent variable. For the maternal provisioning, the number of offspring was designated as the independent variable and the mother's body-mass as the dependent variable.

RESULTS

Female Body-mass vs. Brood Size

The mean body-mass of the females before egg-laying was 257.8 ± 66.6 mg (\pm SD) and females produced a mean of 89.2 ± 23.6 spiderlings ($n = 30$). The number of offspring increased significantly with female body-mass (ANOVA test for linear regression analysis: $r^2 = 0.276$, $df = 1$, $F_{[1,28]} = 10.660$, $p = 0.0029$; Fig. 1).

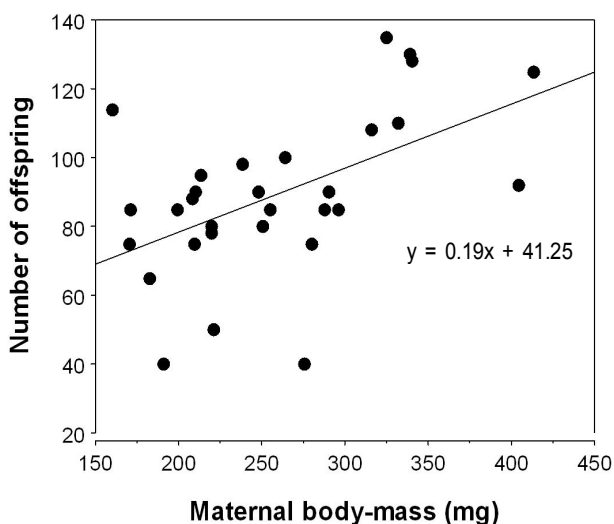


Fig. 1. The relationship between female body-mass and the number of offspring in *Amaurobius ferox* ($n = 30$ clutches).

Investment of Maternal Body-mass Via Trophic Eggs

Mothers did not produce more trophic eggs with increasing numbers of offspring. Mean maternal body-mass before trophic egg-laying was 347.6 ± 66.0 mg, and it was 249.6 ± 65.8 mg after trophic egg-laying. There was also no relationship between maternal body-mass before trophic egg-laying and the number of spiderlings (ANOVA for the regression: $F_{[1,9]} = 1.363$, $p = 0.2729$; Fig. 2-A). Mothers lost an average of 97.9 ± 17.9 mg during trophic egg production, and maternal body-mass loss showed no relationship with the number of spiderlings in the brood (ANOVA for the regression: $F_{[1,9]} = 0.149$, $p = 0.7085$; Fig. 2-B). Mothers transferred a mean of $28.8 \pm 6.5\%$ of their body-mass to their offspring via trophic egg production ($n = 11$). There was also no relationship between the number of spiderlings in the brood (mean \pm SD = 75.5 ± 18.9) and the proportion of body-mass transferred via trophic eggs (ANOVA for the regression: $F_{[1,9]} = 0.272$, $p = 0.6143$; Fig. 2-C). There was also no relationship between the number of spiderlings in a brood and the spiderlings' mean body-mass after consumption of trophic eggs (ANOVA test for the linear regression: $F_{[1,9]} = 0.375$, $p = 0.5554$; Fig. 2-D). The mean of spiderling's body-mass after consumption of the trophic eggs was 0.89 ± 0.10 mg ($n = 11$ broods).

Investment of Maternal Body-mass Via Matrophagy

Larger broods consumed more maternal body materials during matrophagy. Maternal body-mass on the day before matrophagy (252.7 ± 63.9 mg) did not display a significant relationship with the number of spiderlings in the brood (ANOVA for the regression: $F_{[1,9]} = 1.197$, $p = 0.3024$; Fig. 3-A). There was also no relationship between the number of spiderlings in a brood and the spiderlings' body-mass after matrophagy (ANOVA for the regression: $F_{[1,9]} = 1.279$, $p = 0.2873$; Fig. 3-B). The spiderlings' body-mass after matrophagy was 2.13 ± 0.23 mg ($n = 11$ broods). There was the positive relationship between the estimated proportion of maternal body-mass consumed in matrophagy and the number of spiderlings in a brood (ANOVA for the regression: $F_{[1,9]} = 5.230$, $p = 0.0480$; $r^2 = 0.368$, Fig. 3-C). Based on the estimated increase in the spiderlings' body-mass after matrophagy, $39.0 \pm 12.5\%$ of the maternal body-mass was transferred to the offspring during matrophagy.

DISCUSSION

There was a positive relationship between female body-mass and the number of offspring in *Amaurobius ferox*: larger females had larger numbers of offspring. Female body size and the number of offspring are basic components of an organism's life history (Stearns 1992). A positive relationship between maternal body-mass and offspring production has been observed in many oviparous animals

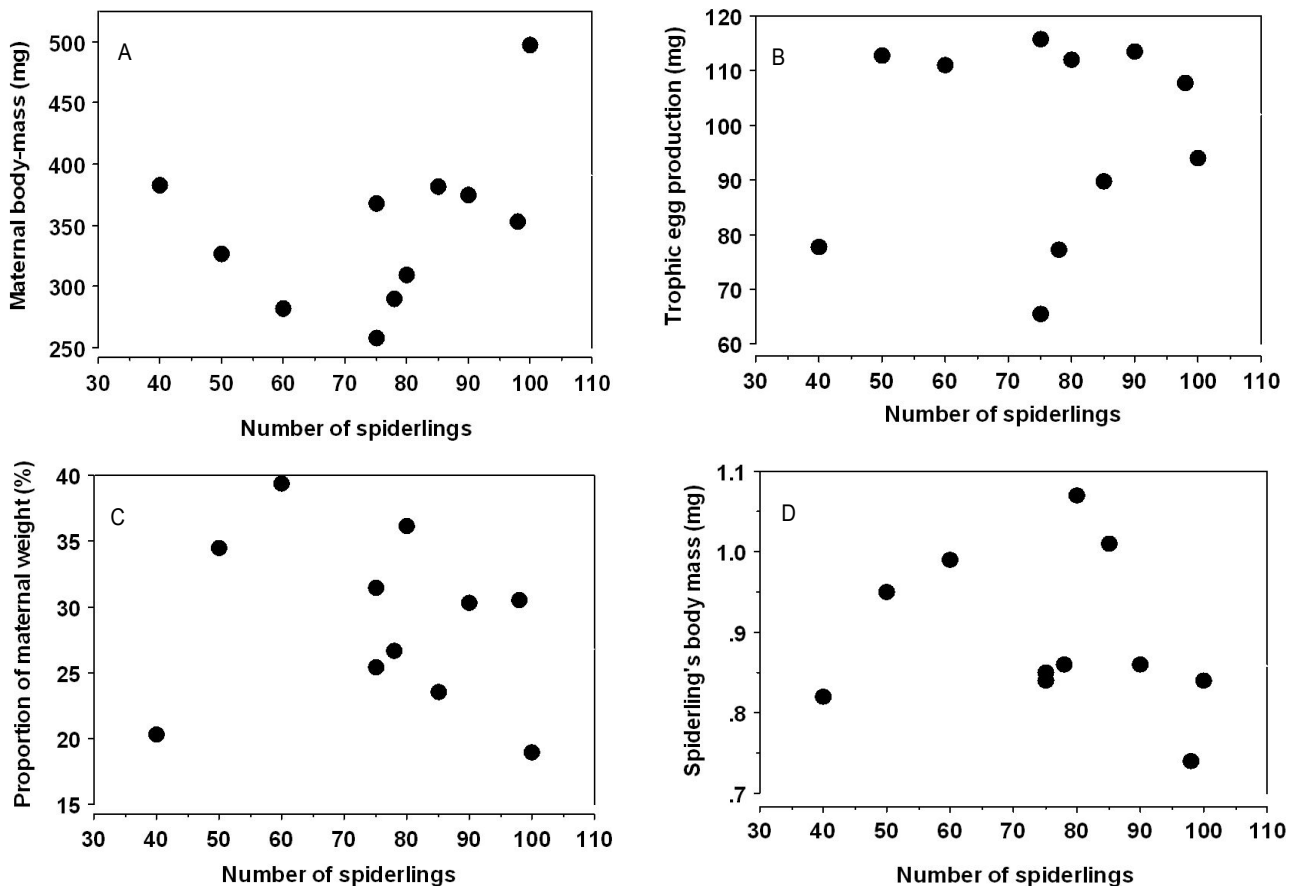


Fig. 2. Trophic egg production of the mothers in relation to the number of spiderlings within their brood ($n = 11$ broods). A: maternal body-mass (mg) before trophic egg-laying, B: trophic egg production (mg) estimated by maternal body-mass loss after trophic egg-laying, C: the percentage of maternal body-mass lost after trophic egg-laying, D: the spiderlings' mean body-mass (in mg) after consumption of the trophic eggs. There were no significant relationships among the parameters.

including spiders (Kessler 1971, Marshall and Gittlemen 1994, Simpson 1995, Skow and Jakob 2003). However, large brood size might not always be better in animals such as *A. ferox* that display obligate matrophagy. During the maternal care period after the emergence of the spiderlings, the maternal body is the only nutrition source for the spiderlings (Kim et al. 2000). Thus the mothers should control their brood size to enable them to allocate the optimal amount of food per capita to their offspring, as the amount of maternal provisions given to each offspring is critical to their fitness and survival (Einum and Fleming 2000, Walker et al. 2003, Dziminiski et al. 2009), and production of large broods without enough resources might result in reduced ability to provision the offspring.

In this study, *Amaurobius* mothers did not produce more trophic eggs when they had larger numbers of offspring. Rather, maternal body-mass loss during trophic egg-laying showed no relationship with the number of spiderlings in the brood. Kim et al. (2000) showed that if mothers are separated from their broods before

laying trophic eggs, they could oviposit a second clutches in average of 9 days after the separation. Under these conditions, they all produced egg sacs, but 60% of the second clutches was aborted or devoured by their own mothers, resulting in significantly decreased numbers of offspring relative to first clutches (Kim et al. 2000). This facultative second oviposition might be an adaptative response to brood loss (see Futami and Akimoto 2005). Trophic egg-laying by *A. ferox* mothers is apparently not calibrated to control the amount of food that each individual offspring receives.

Larger broods of *A. ferox* consumed greater quantities of maternal tissue: there was a positive relationship between the percentage of maternal body consumed during matrophagy and the number of spiderlings within a brood. Matrophagy in *A. ferox* is a precisely-timed collective activity that follows a predictable series of mother-offspring interactions (Kim and Horel 1998). Every individual in the brood shows synchronized swarming behavior toward the maternal body at the moment of matrophagy (Kim and Horel 1998). This

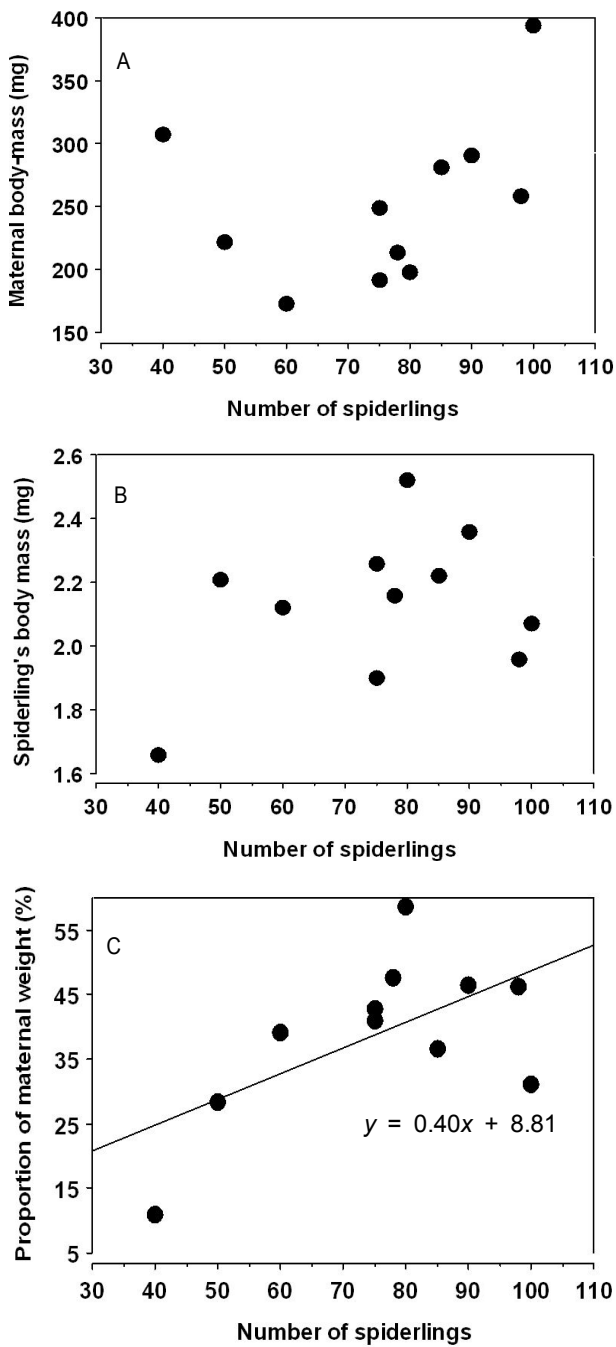


Fig. 3. Matiphagy in relation to the number of spiderlings within a brood ($n = 11$ broods). A: maternal body-mass (mg) on the day before matiphagy, B: mean of spiderling's body-mass (mg) after matiphagy, C: percentage of maternal body-mass consumed during matiphagy, estimated by the increase in the spiderlings' body-mass after matiphagy (ANOVA test for the regression: $F_{[1,9]} = 5.230$, $p = 0.0480$; $r^2 = 0.368$).

behavior might be a form of competition by which individuals seek to maximize their intake. Matiphagy in *A. ferox* results in a 2.5-

fold weight gain in the offspring over their initial mass, advancement of their molting time, and a larger body-mass at dispersal relative to broods denied the opportunity for matiphagy (Kim et al. 2000). *Amaurobius* females are physiologically capable of producing second egg sacs; however, experiments show that net female reproductive output, calculated as the number of surviving midinstar juveniles, is maximized by matiphagy rather than the alternative strategy of abandoning the offspring in order to lay a second clutch (Kim et al. 2000). The amount of food provided to spiderlings through matiphagy in the Australian social crab spider, *Diaea ergandros* (Thomisidae), is positively correlated with the number of surviving spiderlings (Evans et al. 1995). Mothers of the Japanese foliage spider, *Chiracanthium japonicum* (Clubionidae) are also eaten by their offspring at the end of the maternal care period (Toyama 2003). Regardless of size, females of *C. japonicum* were completely consumed by their offspring, and larger females, i.e. those having larger reserves, produced a larger number of offspring (Toyama 2003).

Mothers of *A. ferox* transferred $28.8 \pm 6.5\%$ of their body-mass to their spiderlings via trophic egg-laying, and the increase in the spiderlings' body-mass after matiphagy indicated that $39.0 \pm 12.5\%$ of maternal body-mass was transferred to the spiderlings via matiphagy. Therefore, *A. ferox* females seem to transfer less maternal body-mass to their spiderlings than females of some other spider species, including *Stegodyphus lineatus* (Eresidae), which also displays suicidal maternal care. *S. lineatus* females produce a single small brood with small eggs and provide the spiderlings with regurgitated fluid and later, with their own body contents via matiphagy (Schneider 1995). Salomon et al. (2005) manipulated brood size in order to determine the pattern of resource allocation by female *S. lineatus*: the females provided 95% of their body-mass to the spiderlings via regurgitation and matiphagy. However, the amount of food regurgitated depended on the brood size. Females provided less food when the brood was reduced: females with experimentally reduced broods provided only 13% of their body-mass to their offspring via regurgitation, whereas females with experimentally increased broods and in the control treatments provided 46.1% and 41%, respectively. Larger females regurgitated significantly more food than smaller females.

A matiphagous organism is obliged to invest all of its resources into a single brood and therefore does not experience a trade-off between current and future reproduction. Such a maternal strategy can be favored if future reproduction is highly unlikely either because of ecological constraints such as high predation risk or because of high costs of reproduction (Stearns 1992). *A. ferox* appears to maximize its fitness by transferring its body to its offspring and foregoing future reproductive attempts.

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