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Limited adaptive life-history plasticity in a semelparous spider, *Stegodyphus lineatus* (Eresidae)

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ABSTRACT

Strictly semelparous animals may still benefit from retaining a plastic reproductive strategy. In cases where the current, usually single brood is too small to deplete maternal resources, females could increase their fitness through investing in another clutch. This may not always be possible if females are constrained and cannot switch between different reproductive performances, such as feeding of young and egg development. We investigated the existence of plasticity in the semelparous spider *Stegodyphus lineatus* by drastically reducing brood sizes at different stages of the reproductive cycle. We asked whether: (1) females will be able to produce another clutch while caring for young; (2) production of another clutch is a function of female resources; (3) small broods will be able to benefit from increased female resources. Few females re-laid and those few all had their broods experimentally reduced shortly after hatching. We could not detect a difference in life-history variables between females that re-laid and those that did not. However, producing a new clutch did not prevent females from feeding the remaining offspring from the first brood. Matriphagy occurred only in broods that were reduced shortly before the young normally consume the mother. The timing of the mother's death was a function of the resources the female had left after brood reduction, namely her body mass. Thus, the spiders are generally plastic in that they possess the potential to invest in a second brood. However, in our experiment, this occurred less often than expected. Either incomplete brood reduction occurs too infrequently to act as a selection pressure for an iteroparous strategy or our reduction was not drastic enough to achieve the expected result.

Keywords: brood reduction, plasticity, semelparity, spider, suicidal brood care.

INTRODUCTION

A semelparous organism invests all its resources into a single reproductive event with the consequence that the trade-off between current and future reproduction is removed (Cole, 1954). Such a strategy is favoured if future reproduction is highly unlikely to occur either

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because of ecological factors such as high predation risks or because of high costs of reproduction (Charnov and Schaffer, 1973; Roff, 1992; Stearns, 1992).

Life-history strategies tend to show a degree of plasticity, enabling the organism to react flexibly to varying environmental conditions. Accordingly, semelparity in many organisms is not strict but equivalent to facultative iteroparity with certain environmental conditions that will favour a semelparous life history while others select for iteroparity (Tallamy and Brown, 1999). Hence, both strategies must not be considered as mutually exclusive alternatives but as strategies on a continuous scale. However, such an optimal plasticity may not be realized under all conditions (Ricklefs and Wikelski, 2002). Causes for a lack of plasticity are phylogenetic or physiological constraints (Ricklefs and Wikelski, 2002).

In arthropods, semelparity and brood care are often linked (Tallamy and Brown, 1999). However, even though brood care reduces offspring mortality, complete or partial brood failure may still occur. Given a probability of failure, a semelparous animal should retain its ability to reproduce if the first attempt fails or does not guarantee a sufficient fitness return. Selection should favour behavioural plasticity, allowing for adaptive decisions of whether to invest all resources into a single brood that is extremely small or to reallocate resources into another reproductive event. This will be especially advantageous if costs of reproduction have not been expended yet (i.e. early in the reproductive cycle).

The eresid spider, *Stegodyphus lineatus*, is annual and semelparous. Females produce a single clutch and feed the young via regurgitation after they emerge from the egg sac (Kullmann *et al.*, 1971). Brood care is suicidal and ends with matriphagy, where the mother is sucked dry by her young. Matriphagy usually occurs 2 weeks after the young are released from the egg sac. Young benefit from brood care through an increased body size, which improves survival over winter (Schneider, 1996a). In an experimental field study, we removed the young from their mother shortly before matriphagy would have occurred and we showed that females are able to lay eggs again (Schneider and Lubin, 1997a). Thus, we know that females retain their capacity to produce eggs until the end of brood care. However, they were only able to raise a second brood if they were protected from predators. Most of the adult mortality was explained by parasitism of a wasp specialized on adult female *Stegodyphus* (El-Hennawy, 1987; Henschel *et al.*, 1996). In addition, high costs of brood care through regurgitation feeding may have further increased mortality. In a model, we calculated that there should be a threshold in brood size below which it does not pay the female to sacrifice her life for such a small brood (Schneider and Lubin, 1997a). If females lose most of their brood or if the hatching rate is low (both cases occur in nature), they will maximize their fitness by producing another clutch as quickly as possible while raising the remaining young to independence. In nature, however, we never observed that a female had young and eggs in her nest at the same time.

In another experiment, young were fostered out to females of different reproductive states and only females with young of their own fed young from other females (Schneider, 2002). This suggested that a physiological maturation process determines whether females care for eggs or feed young. Such a mechanism is likely under hormonal control and may hinder the switch from feeding hatchlings to developing eggs again.

In this study, we wished to determine whether females with very small broods would opt for a second reproductive event and whether such a decision would influence the occurrence of the two major components of brood care: regurgitation feeding and matriphagy. We drastically reduced broods of females 2, 5 and 10 days after the young emerged from the egg sac. We monitored the nests for the appearance of new egg sacs, for occurrence of matriphagy and weighed young and females after fixed time intervals to establish whether regurgitation feeding occurred. We expected that females would produce a second clutch depending on the relative reduction of their brood and their own body condition. We further expected that an early reduction should lead to a higher frequency of iteroparity than a late reduction.

MATERIALS AND METHODS

During March and April 1999, female and male *Stegodyphus lineatus* were collected as subadults along the Jerusalem to Jericho road in the Judean desert, Israel, and translocated to a screened insectary together with their nests. All nests were inspected daily and the day of their final moult was recorded. Males were removed from the insectary as soon as they matured to prevent them from leaving their nests for mate search. This was necessary for us to control when and how often females mated. After maturation, mated females were monitored for the appearance of egg sacs.

Either 2 or 10 days after the young hatched, nests were removed from the insectary and transferred to plastic cups (10 cm in diameter and 5 cm high) in the laboratory. Females were measured and weighed and young were counted (Table 1). We used an electronic balance (Kern 430/21) with an accuracy of 0.1 mg. Female condition was calculated by dividing body mass by fixed body size (prosoma width).

Thirty-eight females were randomly selected and their broods were reduced to approximately five young either 2 ($n = 9$) or 10 days ($n = 18$) after hatching. We did not always achieve an exact reduction to five young because we sometimes overlooked spiderlings in the densely woven silk of the nest. We opened the nest by cutting open the entire silk tube and we sewed it back together after the spiderlings were removed. The female and the remaining five young were carefully put back into the repaired tube and left undisturbed for a few days. The 2-day reduction was checked after 13 days and the 10-day reduction after 5 days, so that we obtained weights for day 15 after hatching for all spiderlings. At this time we re-opened the nest, counted and weighed the spiderlings and the female. We then checked the nests each day until day 35 after hatching for the appearance of egg sacs or the occurrence of matriphagy. Fourteen females were assigned as controls; they were handled in the same way as the treatments but all young were given back to their mothers. Females with young were not fed. This is not unnatural because females with young usually do not maintain a web.

In 2002, we repeated the reduction after 2 days of hatching with 20 broods to increase the sample size. In addition, we reduced 20 broods 5 days after hatching (Table 1). We were

Table 1. Basic data on females and broods in the different treatments (mean ± standard error)

	Female mass (g)	Female prosoma (mm)	Brood size	*n*
2-day reduction, 1999	0.533 ± 0.039	4.25 ± 0.11	58.90 ± 6.74	9
2-day reduction, 2002	0.637 ± 0.048	4.13 ± 0.06	70.95 ± 8.85	20
5-day reduction	0.679 ± 0.044	4.25 ± 0.40	79.10 ± 8.59	20
10-day reduction	0.519 ± 0.032	4.28 ± 0.11	45.70 ± 3.85	18
Control 1999	0.466 ± 0.037	4.11 ± 0.12	40.29 ± 6.91	14

Note: Females were measured and weighed after the egg sac hatched.

unable to return to our previous collection site in the Judean desert and instead we collected spiders from the road-side near Tel Arad, from a population that is genetically similar to the Judean desert populations (J. Johannesen, in prep.). Nevertheless, we cannot rule out potential intrinsic differences in behaviour between the females used in the 2 years. In principle, we followed the same protocol as in 1999, but weighed spiderlings and females 13 days after hatching rather than 15 days as before and terminated the experiment 25 days after hatching. To neutralize this discrepancy in the 2-day reduction experiment, we used mass gain per day in the analysis. Both treatments were followed for 20 days after the reduction and nests were inspected daily for new egg sacs and matriphagy.

Spiderlings that were removed were used for different experiments and given to foster females. After the experiment, surviving Tel Arad spiders were released back into their original populations and Judean desert spiders were kept as voucher specimens.

RESULTS

In the 2-day reduction experiment, five females produced a second clutch within 25 days after the reduction. Four of these second clutches were from the 1999 experiment and one from 2002. Neither in the 5-day reduction experiment nor in the 10-day reduction experiment did females produce second clutches.

Within the observation period, matriphagy only occurred in the 10-day reduction experiment. Ten of 18 females in this treatment were consumed by their young within 22 days after the reduction.

In three broods no spiderlings survived. Complete failures only occurred in the 2-day reduction experiment.

Two-day reduction

In the two years, broods of 29 females were reduced to approximately five young on the second day after hatching. Broods were monitored for 35 days after hatching in 1999 and 20–30 days in 2002. In 1999, four females produced a replacement clutch after 14–18 (median 14.5) days. In 2002, only a single female laid a second clutch 25 days after the treatment. Perhaps because of low statistical power, we could not detect a statistically significant difference in any measured variable between these five females and those that did not lay eggs again (Table 2). The relative reduction of the brood in these five females was somewhat more extreme, with only 7% of the brood left compared to a mean of 14% in the other broods, and females that re-laid tended to be larger but the differences were not significant.

Interestingly, even though very few females re-laid, the previous young of these females grew. This demonstrates that these females initiated egg development and fed their young at the same time. The timing of the second oviposition varied between females but the small number of females that re-laid does not permit a detailed analysis of causes for the variation in the timing of re-laying.

Ten-day reduction

The broods of 18 females were reduced to approximately five young 10 days after hatching. Matriphagy occurred in 10 of these broods within 22 days after the treatment. None of the

Table 2. Comparison of variables between females that did not produce a second clutch and those that did in the 2-day reduction treatment (mean ± standard error)

	Second eggs ($n = 5$)	No eggs ($n = 24$)	Z	P
Female mass (g)	0.63 ± 0.05	0.60 ± 0.04	0.55	0.58
Female prosoma (mm)	4.4 ± 0.11	4.1 ± 0.06	1.74	0.08
Female condition	0.14 ± 0.01	0.15 ± 0.01	0.09	0.93
Initial brood size	72.6 ± 6.67	66.1 ± 7.72	0.49	0.62
Proportion brood retained	0.07 ± 0.01	0.14 ± 0.03	−0.84	0.40
Mass of young, day 12 (mg)	4.61 ± 0.80	5.76 ± 0.66	−0.52	0.60
Female mass loss, day 10 (g)	−0.14 ± 0.04	−0.08 ± 0.01	−1.61	0.11
Gain of young per day (mg)	0.11 ± 0.02	0.12 ± 0.02	−0.44	0.66

Table 3. Comparison of variables between females in the 10-day reduction experiment that were consumed by their young and those that survived

	Matriphagy ($n = 10$)	No matriphagy ($n = 8$)	Z	P
Female mass (g)	0.52 ± 0.02	0.52 ± 0.07	−0.13	0.89
Female prosoma (mm)	4.3 ± 0.12	4.2 ± 0.20	−0.40	0.69
Female condition	0.12 ± 0.01	0.12 ± 0.01	−0.22	0.82
Initial brood size	51.3 ± 4.62	38.8 ± 5.83	−1.51	0.13
Number of young left	7.6 ± 0.85	6.63 ± 0.65	−0.74	0.46
Proportion brood retained	0.16 ± 0.02	0.27 ± 0.11	0.49	0.62
Mass of young, day 15 (mg)	8.17 ± 0.96	6.78 ± 0.98	−0.31	0.76
Female initial investment	1.36 ± 0.12	1.03 ± 0.16	−1.38	0.17
Resources left per young (mg)	0.05 ± 0.01	0.054 ± 0.01 ($n = 6$)	0.27	0.79

Note: Female initial investment is calculated as the mass of the entire brood at day 10 divided by the condition of the female at hatching of her brood. Resources left per young is the mass of the female at day 10 divided by the number of young she retained.

measured variables differed significantly between females that died by matriphagy and females that were not consumed by their young (Table 3). Again, small sample sizes make a comparison difficult. However, the timing of matriphagy was explained by the resources the females had left for these young, namely by her body mass at the day of reduction ($r^2 = 0.55$, $F_{1,8} = 9.9$, $P < 0.02$; Fig. 1).

None of the surviving females laid a second clutch, but three females died after 29–31 days. These deaths were not included in the matriphagy sample because the young were in an advanced stage already, beyond the stage at which matriphagy normally occurs. These females probably died of causes other than brood care.

DISCUSSION

Contrary to our predictions, very few females laid a second clutch if their brood was drastically reduced to only five young. Dying for such a small brood would bring very small fitness returns when compared to an iteroparous strategy of producing a second

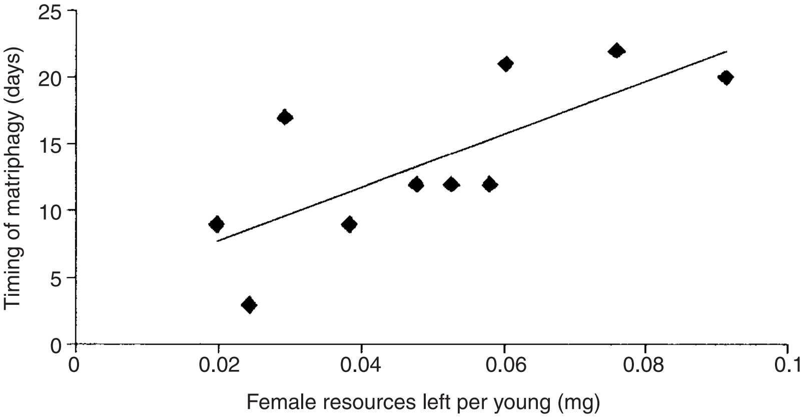

Fig. 1. Timing of matriphagy measured in days after hatching as a function of the female's resources left per remaining young. The latter is calculated as: the female's mass at day 10 divided by the number of young that were left after the reduction (day 10).

brood, given that there was a realistic chance of succeeding. An iteroparous strategy, however, would only be selected for if the development of new eggs does not prevent care for the current brood, no matter how small it is. Our experiment revealed two main results: (1) *Stegodyphus lineatus* females can produce a second clutch and at the same time will continue to feed young; (2) broods that were reduced early did not consume the body of the mother. Hence, one could expect a conditional strategy of re-laying in the experimental context.

The fact that five females produced a clutch while they continued to feed the remaining young suggests that regurgitation of food to the young does not physiologically constrain further egg development or oviposition. In an earlier experiment, we showed that females that had their entire brood removed were able to lay eggs again (Schneider and Lubin, 1997a); we can now extend this to females that are feeding young. The potential to re-lay, combined with the fact that spiders generally store sperm over long periods of time, suggests that we can exclude sperm depletion as a potential constraint on re-laying. There was a delay of at least 2 weeks until a replacement clutch appeared. This time lag is identical with that found for females whose eggs or young were removed entirely (Schneider and Lubin, 1997a,b), which suggests that about 2 weeks is generally required for the completion of egg development. The timing of egg-laying, however, could not be analysed any further with our limited data set.

A previous field experiment showed that females survived to complete a second reproductive event only if they were protected from predators (Schneider and Lubin, 1997a). Adult females suffer a constant daily mortality risk due to predation (Schneider, 1996b). Hence the longer they take to complete their reproduction, the less likely it becomes that they will survive until matriphagy can occur. However, in the field experiment we removed the broods shortly before matriphagy occurred (10 and 13 days after hatching), so that females had already expended most of their resources in raising the first brood. Therefore, it is reasonable to expect that the chances of reproducing again would be greater for females that lost their broods in an earlier stage. Even though the probability of successfully raising a second clutch may still be small, the slightest chance of success should select for facultative iteroparity, especially if it does not require deserting the first brood.

As predicted, the probability of re-laying was highest in the 2-day reduction experiment, while later reductions did not elicit a re-laying response. It is surprising that so few females re-laid and that those few females who did lay eggs again did not differ in any of the measured life-history parameters from the other females. However, the latter may be due to small sample sizes. A possible explanation is that the early plasticity apparent in the 2-day reduction experiment may later become constrained through physiological adaptations to brood care. It is also possible that the spiderlings in the nest somehow inhibit the female's ability to re-lay eggs. This, however, would only be adaptive if the young received no indirect fitness benefits from the replacement clutch. However, as females store sperm and do not mate again, young of successive clutches are related and, therefore, indirect fitness benefits will be present. Finally, the question remains whether an iteroparous strategy will bring any additional fitness returns under natural conditions of high predation risk. In a field study, 64% of 127 broods were attacked by predators and 48% of these attacks had fatal consequences (Schneider, 1996b).

Small broods did not consume their mother in the 2-day or in the 5-day reduction experiment, suggesting that they were not able to utilize all of the maternal resources during the regurgitation phase of maternal care. Matriphagy only occurred when broods were reduced late and females had already invested most of their resources in the full brood. The timing of matriphagy was a clear function of female resources available per young. Consequently, in earlier reductions, the interests of females and young should coincide, in that fitness would be maximized through the production of a second clutch. In a previous study, the timing of matriphagy was best explained by maternal rather than offspring variables and it was suggested that it is under maternal control (Schneider, 2002). The reduction experiment corroborates this interpretation, in which case it is even more surprising that females whose broods were reduced after 2 or 5 days did not opt for another reproductive event. Whether this is adaptive or a physiological constraint remains unclear.

In conclusion, despite the ability to raise a small first brood while producing another clutch and the fact that a small brood will not consume all maternal resources, relaying in *Stegodyphus lineatus* was surprisingly infrequent. The reasons for the relative lack of plasticity in the life history of *S. lineatus* remain to be studied. To our knowledge, no other study has experimentally investigated plasticity in semelparity within a species. This is perhaps so because the evolution of a semelparous life history is usually seen as irreversible, as suggested for salmonid fishes (see Crespi and Teo, 2002). However, it remains astonishing that *S. lineatus* spiders retained a plasticity in reproduction without being able to realize their options in the given context.

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