Predation and foraging costs of carrying eggsacs of different mass in the wolf spider *Pardosa milvina*

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(Accepted: 2 June 2007)

Summary

Female *Pardosa milvina* wolf spiders carry large eggsacs. We quantified the effects of carrying eggsacs on foraging success and susceptibility to predation. In addition to monitoring individuals carrying natural eggsacs, we induced females to carry artificial eggsacs of varying mass. We determined the propensity of females to attach eggsacs or plastic beads of various sizes. We then quantified prey capture success and the avoidance of the predatory wolf spider, *Hogna helluo*, for *Pardosa* with and without eggsacs or plastic beads attached. Females attached their own eggsacs significantly more than plastic beads of equal mass and attached artificial eggsacs 10 times larger than natural eggsacs significantly less often than smaller plastic beads (ones equal to or 2.7 times the size of natural eggsacs). Females carrying real or artificial eggsacs of any mass captured fewer prey, but prey capture success did not vary among females with different-sized eggsacs. Except females of the 10 × eggsac treatment, individuals carrying an eggsac suffered significantly greater predation compared to females without eggsacs. Eggsac transport carries significant predation and foraging costs, but we found little evidence that carrying heavier eggsacs incur incrementally greater increases in predation risk or decreased foraging efficiency than carrying lighter eggsacs.

Keywords: reproductive costs, forage, prey, Lycosidae, egg case.

Introduction

Various forms of parental investment positively impact offspring fitness, however such benefits may be offset by either incremental decreases in the

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Behaviour 144, 1003-1018
Also available online - www.brill.nl/beh

residual reproductive value of the parent or immediate costs that may compromise survival (reviewed in Clutton-Brock, 1991). The optimal clutch size for animals that care for their young is often strongly influenced by whether the costs change incrementally with increasing clutch size or are fixed and largely independent of offspring number. In many cases, it is not obvious which costs are incremental and which costs are fixed with increasing clutch size. For example, parental foraging by lesser snow geese decreases linearly with increasing brood size, but vigilance for predators increases with offspring number to broods of five and then drops thereafter (Williams et al., 1994).

Many animals invest in offspring by protecting early developmental stages (Brokordt et al., 2003). Energetic and time costs associated with protecting embryos or young can be significant for nesting species (FitzGerald et al., 1989; Guderley & Cubillos, 1998), but these costs may not necessarily increase with offspring number if the parents only offer protection from predators. Unlike species that guard young at a fixed location, the cost function for protecting clutches of different sizes may be quite different for those species that actively transport their offspring. In these cases, carrying offspring may be associated with reduced locomotor efficiency, which, in turn, may compromise both foraging success and predator avoidance (Bauwens & Thoen, 1981; Winfield & Townsend, 1983; Crowl & Alexander, 1989; Cooper et al., 1990; Sinervo et al., 1991; Shaffer & Formanowicz, 1996; Kight & Ozga, 2002).

The locomotor costs of carrying offspring or eggs may be quite high among terrestrial arthropods (Moffet & Doell, 1980; Shaffer & Formanowicz, 1996; Lardies et al., 2004). Seven orders of arachnids are known to actively transport their young as they move through the environment (Polis & Sissom, 1990). However relatively few studies have investigated the costs associated with offspring transport among arachnids. Shaffer & Formanowicz (1996) found that sprint speed slows proportionately with clutch sizes among scorpions (Shaffer & Formanowicz, 1996), but the cost of reduced sprint speed in the form of decreased prey capture or escape from a live predator remains largely untested. Further, it remains unknown if increasing numbers of offspring cause incremental decreases in foraging success and incremental increases in predation risk, or whether these costs are fixed and are independent of offspring number.

Wolf spiders (Lycosidae) present a model system for testing hypotheses regarding the cost of parental care because females invest heavily in brooding their young. Adult females wrap their mass of eggs by fibrous sheets of silk to construct an eggsac (Foelix, 1996). The eggsac is then attached to the spinnerets and carried for twelve to over thirty days (Eason, 1964). After several weeks a hole in the seam of the eggsac is torn and spiderlings emerge and are carried by their mother for an additional period of time ranging from three days to two or more weeks (Fujii, 1977; Persons & Lynam, 2004). Both the size and weight of these eggsacs may limit the ability of females to capture large prey and avoid predation (Marshall & Gittleman, 1994); as such, these selection pressures may impose an upper limit to eggsac mass. Because wolf spiders attach their entire eggsac to their spinnerets by a small silk strand, females have the option of immediately dropping the eggsac while grappling with large prey or escaping a predator. However, dropping an eggsac may result in losing it, and because the spiderlings can exit the eggsac only by the female opening it, this may result in the death of all spiderlings (Fujii, 1977).

Pardosa milvina (Araneae, Lycosidae) are active cursorial predators commonly found in agroecosystems (Marshall & Rypstra, 1999; Barnes et al., 2002; Persons et al., 2002). Adult female *Pardosa* attach and carry eggsacs that weigh an average of 72% of their post-reproductive body weight (see Results, $N = 165$). While carrying eggsacs, females continue to be highly mobile while feeding on various ground-dwelling arthropods that may be equal or greater than their own body weight. During this time females may be particularly susceptible to a larger co-occurring predatory wolf spider, *Hogna helluo* (Araneae, Lycosidae). These predators are abundant in the same habitats (Marshall & Rypstra, 1999) and voraciously feed on *Pardosa milvina* (Persons et al., 2001, 2002).

Like other lycosids, *Pardosa* occasionally drop their eggsacs and may mistakenly attach foreign objects such as snail shells or small pieces of dried soil to their spinnerets when they cannot locate their own eggsac (O'Connor, 1896; Locket & Marsh, 1957). We took advantage of this phenomenon to experimentally induce female spiders to attach artificial eggsacs of different weights. We then measured the ability of *Pardosa* females with and without natural eggsacs or plastic beads attached to their abdomen to capture prey or evade predation by *Hogna*. In this way we could quantify the specific costs of eggsac transport as well as any incremental shifts in those costs as eggsac size increased.

Material and methods

General collection and maintenance

Pardosa milvina with eggsacs were collected June through September from within and around corn and soybean fields in Snyder County, Pennsylvania, USA and Butler County, Ohio, USA and brought into the laboratory. All spiders were placed individually in translucent plastic containers (8 cm in diameter; 5 cm walls) with 2.5 cm of moist peat moss covering the bottom. While in the laboratory, *Pardosa* were provided with five 5-10-day-old cricket nymphs (*Acheta domesticus)* each week and were held at 23-25°C on a 13:11 light/dark photoperiod.

Eggsac selection

In a no choice experiment, we quantified the propensity of *Pardosa* females from the Pennsylvania population to attach different sized plastic beads or their own eggsacs after they had been removed. We carefully removed eggsacs with entomological forceps and weighed them. Each female was then placed in a 45 dram plastic vial (5 cm diameter $\times$ 8.5 cm h) with her own eggsac (3.94 mm diameter $\pm$ 0.035; 12 mg $\pm$ 2 S.E.; $N = 165$) or a single black plastic spherical bead either 3 mm (11 mg), 4 mm (27 mg) or 6 mm (104 mg) in diameter. The female was left with a water source for 12 h at which time we recorded whether she had attached the bead or eggsac to her spinnerets or not. Acceptance frequencies among the 165 spiders were compared with the chi-squared goodness of fit test.

Eggsac effects on prey capture

In order to standardize hunger, we provided field caught female *Pardosa* from Ohio and Pennsylvania with as many crickets as they could consume over a 24-h period. We then removed any uneaten crickets and held the spiders for three days with a water source but no food. At this time, the eggsac diameter of the spiders from the Ohio population was measured using an ocular micrometer. Twenty of these females were selected at random and their eggsacs were removed by squeezing where it was attached to the spinnerets with entomological forceps. Another 58 Ohio females were held and manipulated but their eggsacs remained intact. The same spiders tested in the no-choice eggsac selection experiment ($N = 165$) were also used to measure foraging success with artificial or natural eggsacs. As indicated above, we removed the eggsacs from all of the Pennsylvania spiders and placed each female in a 45 dram vial with no item to attach, its own eggsac or a plastic bead, 3 mm, 4 mm or 6 mm in size (see Table 1 for sample sizes). Spiders were given 12 h to attach the bead or eggsac and, in those treatments that required it, only those that attached the item were used in subsequent experiments.

Foraging success was quantified in cylindrical plastic containers (9 cm diameter; 7 cm walls) with 2 cm of moist peat moss covering the bottom. Each female *Pardosa* was released into the container and allowed to acclimate for 30 min. A single cricket (selected to be half the mass of the spider) was introduced under a translucent plastic vial (2 cm diameter). After allowing 5 min to acclimate, we lifted the vial and recorded if and when the spider killed the cricket in the following 2-h time period. For the experiment using artificial eggsacs (Pennsylvania spiders), it was necessary to use the same spiders in subsequent predation experiments. To maintain hunger levels across treatments for those spiders, we did not allow spiders to consume the crickets. We gently removed captured crickets from the spider's chelicerae and gently touched the chelicerae of spiders that did not capture crickets with forceps to standardize for any handling effects. We analyzed the Ohio experiment with natural eggsacs that varied in size and the Pennsylvania experiment with artificial and natural eggsacs separately. For both experiments, we compared the number and timing of cricket capture among treatments using a non-parametric survival analysis with a Kaplan-Meier product limit estimator (see Lee, 1992; Moya-Laraño & Wise, 2000) and tested for equivalence of survival functions based on a Mantel-Cox (log-rank) test (Statview®, 1999). For the Ohio experiment we also tested for an effect of the size of the natural eggsacs on the likelihood of prey capture using a logistic regression.

Eggsac effects on predator avoidance

Parallel experiments were conducted using Ohio and Pennsylvania spiders in order to explore the effects of eggsac size on the ability of *Pardosa milvina* females to escape predation. To measure predation risk of *Pardosa* by the larger wolf spider, *Hogna helluo*, an additional 81 female *Pardosa* were collected from the Ohio fields and brought into the laboratory for a minimum of 5 days. These spiders were maintained in the laboratory, fed and manipulated as described above for tests of predator avoidance ability. We removed the eggsac from 20 of them and simply measured the eggsac of the other 61 females. For the experiment with artificial eggsac treatments (Pennsylvania spiders) we used the *Pardosa* that had participated in the prey capture experiment to quantify their ability to avoid predation.

Females of the larger co-occurring wolf spider *Hogna helluo* (Araneae, Lycosidae) served as predators for both experiments because it is known to be a voracious predator of *Pardosa* (Persons et al., 2001; Barnes et al., 2002; Lehmann et al., 2004). Subadult or adult female *Hogna helluo* were collected from the same habitats as *Pardosa* (for both Ohio and Pennsylvania populations respectively) and were maintained in the laboratory for at least 2 weeks prior to being used as predators. Each *Hogna* was allowed to consume as many crickets as possible in 24 h within laboratory containers 9 cm in diameter. We then removed any remaining crickets and held the spiders for 3 days with a moisture source but no additional food to standardize hunger levels.

Pardosa were left in the cylindrical plastic container (9 cm in diameter) for 2 h (for spiders participating in both trials this was the same container used in the foraging trial). Female *Hogna* were introduced under a plastic vial (3 cm in diameter) and allowed to acclimate for five min. We then lifted the vial and observed the interactions between the two spiders for two hours. As above we analyzed the results from the natural eggsac experiment (Ohio population) and artificial eggsac treatments (Pennsylvania population) separately. For both, we compared *Hogna* predation on *Pardosa* in different eggsac treatments using a non-parametric survival analysis with a Kaplan-Meier product limit estimator and tested for equivalence of survival functions based on a Mantel-Cox log-rank test. For the Ohio experiment we also tested for an effect of the size of the natural eggsac on the likelihood of prey capture using a logistic regression.

Results

Eggsac selection

All of the *Pardosa* females given the option of reattaching their own eggsac did so which was not true for those provided plastic beads ($\chi^2 = 18.079$, $p = 0.0004$; Table 1). Among artificial eggsac treatments, there were also significant differences in preference ($\chi^2 = 6.821$, $p < 0.05$; Table 1); large 6-mm beads were the least likely to be attached (Table 1).

Table 1. Sample sizes for each artificial eggsac experiment. Eggsac selection indicates the number and percent of *Pardosa* that reattached their own eggsac or attached a bead in different size classes within 12 h. Eggsac dropping during prey capture is the number of spiders in each treatment that dropped their eggsac while capturing a large domestic house cricket. Eggsac dropping during predator avoidance is the number of spiders that dropped their eggsac while trying to avoid predation by an adult female *Hogna*.

Eggsac treatment	Eggsac selection			Eggsac dropping during prey capture		Eggsac dropping during predator avoidance	
	Number offered	Number attached	Percent accepted	Number tested	Number lost	Number tested	Number lost
Own eggsac	22	22	100	20	1	19	0
3-mm bead	46	32	69.6	24	0	24	1
4-mm bead	44	34	77.3	31	1	30	2
6-mm bead	53	28	52.3	21	5	16	2
No eggsac	–	–	–	34	–	34	–

Eggsac effects on prey capture

When *Pardosa* females were carrying something attached to their spinnerets, prey capture was significantly reduced whether it was a naturally produced eggsac (Ohio natural eggsac vs no eggsac experiment: Mantel Cox, $\chi^2 = 5.133$, df $= 1$, $p = 0.0235$; Table 2; Figure 1A) or an artificial bead of any size (Pennsylvania bead experiment: Mantel-Cox, $\chi^2 = 46.335$, df $= 4$, $p = 0.0001$; Figure 2A). However there was no significant difference in the timing or frequency of cricket capture among the various eggsac or bead treatments (Figures 1A, 2A). Statistical differences in survival and prey capture were attributed entirely to higher prey capture levels among unencumbered females (Figure 2A). A few spiders dropped the item they were carrying during this experiment but the numbers were not large enough to compare statistically (Table 1). The natural eggsacs for spiders in foraging trials ranged from 6.0 to 25.3 mg (mean 13.7 $\pm$ 0.6 mg), however the probability of cricket capture was not related to eggsac size (Logistic regression, $\chi^2 = 0.217$, df $= 1$, $p = 0.641$).

Table 2. The number of adult female *Pardosa milvina* with and without eggsacs that captured crickets or escaped predation by *Hogna helluo*. Mean eggsac mass ± S.E. of *Pardosa milvina* that captured crickets or were captured by *Hogna helluo*.

	Number (%)		Eggsac mass (mg)	
	Capture	No capture	Capture	No capture
Prey capture experiment				
Intact eggsac	40 (69)	18 (31)	13.9 ± 0.7	13.3 ± 1.3
Eggsac removed	18 (90)	2 (10)	13.6 ± 1.3	13.0 ± 4.0
Predator escape experiment				
Intact eggsac	34 (55.7)	27 (44.3)	13.7 ± 0.7	14.3 ± 1.5
Eggsac removed	11 (55)	9 (45)	14.5 ± 1.4	11.9 ± 1.9

Eggsac effects on predator avoidance

When *Pardosa* females were carrying something attached to their spinnerets, their ability to escape a predator was significantly reduced whether it was a naturally produced eggsac (Ohio Natural eggsac vs no eggsac experiment: Mantel Cox, $\chi^2 = 7.241$, df = 1, $p = 0.0071$; Figure 2A) or an artificial bead (Pennsylvania bead experiment: Mantel-Cox, $\chi^2 = 9.809$; df = 4, $p = 0.0438$; Figure 2B). Not surprisingly, females without eggsacs had higher survivorship (Figure 2A,B). Pairwise comparisons conducted on the artificial bead experiment revealed that, although no-eggsac female survival was significantly better than the eggsac and most of the bead treatments, there were no differences between survival of females carrying the 6-mm bead and any other treatment (Figure 2B). Five of the *Pardosa* dropped their beads in their interactions with *Hogna*, but the frequency of this behavior was insufficient to compare statistically (Table 1). For those spiders carrying eggsacs that they produced naturally, the probability of being captured was not related to eggsac size (Logistic regression, $\chi^2 = 0.095$, df = 1, $p = 0.758$). The size of carried eggsacs ranged from 5.8 to 25.5 mg (mean 12.8 ± 0.6 mg).

Discussion

We found significant foraging and predation costs associated with carrying an eggsac in *Pardosa milvina*. Surprisingly, we found little evidence that

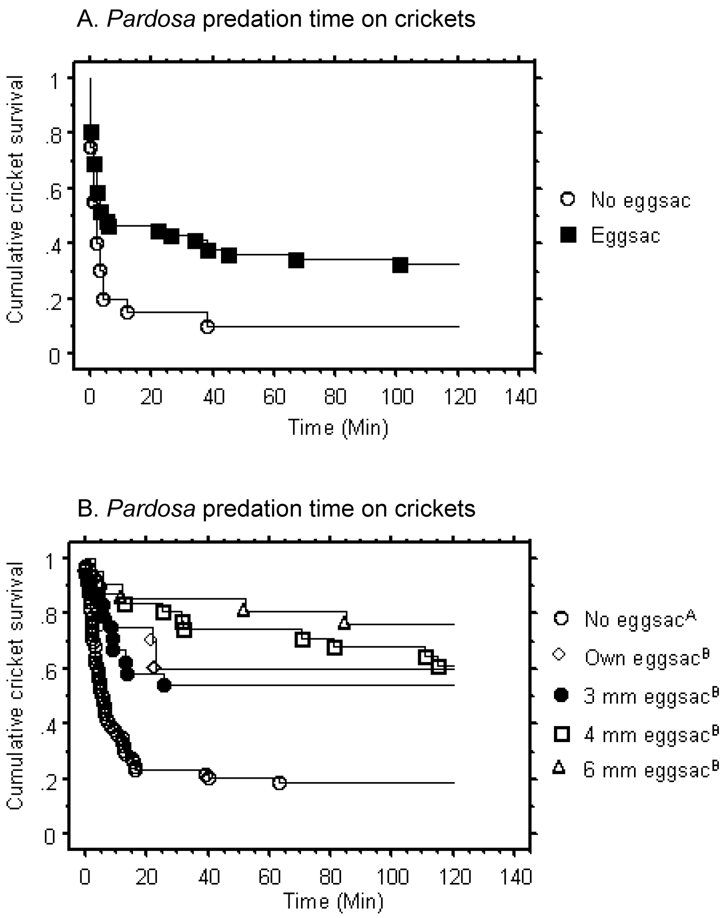

Figure 1. (A) Cumulative proportion of surviving house crickets exposed to an adult female *Pardosa milvina* carrying or not carrying an eggsac. Each point on the graph indicates a predation event and a subsequent decrease in the number of surviving crickets of that treatment. (B) Cumulative proportion of surviving house crickets exposed to an adult female *Pardosa milvina* carrying or not carrying a natural or artificial eggsac of a particular mass. Each point on the graph indicates a predation event and a subsequent decrease in the number of surviving crickets of that treatment. Different letters superscripted next to each treatment group indicate treatments that were significantly different from each other after Mantel-Cox (log-rank test) pair-wise comparisons at an alpha level of 0.05.

such costs are incrementally higher with increasing eggsac mass, but rather the significant differences in prey capture and predator survival occurred between those carrying any eggsac at all and unencumbered females.

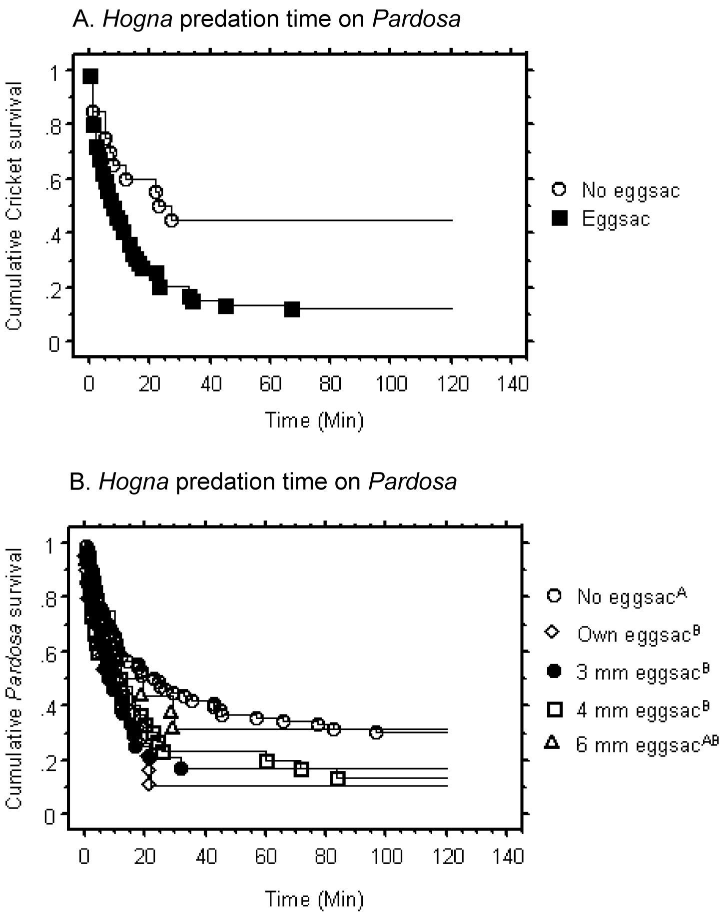

Figure 2. (A). Cumulative proportion of surviving adult female *Pardosa milvina* in the presence of live *Hogna helluo*. Treatments include females with and without eggsacs. (B) Cumulative proportion of surviving adult female *Pardosa milvina* in the presence of live *Hogna helluo*. Treatments include females with black plastic beads of different mass (3 mm, 4 mm and 6 mm, respectively), the spiders own eggsac (own), or adult females that have had their eggsacs removed prior to the experiment (no eggsac). Different letters superscripted next to each treatment group indicate treatments that were significantly different from each other after Mantel-Cox (log-rank test) pair-wise comparisons at an alpha level of 0.05.

Our study on eggsac acceptance revealed that *Pardosa* females were more likely to reattach their own eggsac than they were to attach an artificial eggsac of any type. However, when not presented with a real eggsac, acceptance rates of plastic beads were still greater than 50%, suggesting that the ability to recognize an eggsac is not particularly well developed and females are prone to make errors when their own eggsac is lost. Among females that accepted foreign objects in place of their own eggsacs, there was only weak discrimination based on size or weight. The 4-mm bead closely matched the average diameter of a real eggsac, while the 3-mm bead was very similar in weight. Because spiders chose both eggsac types with similar frequency, neither weight nor overall size took precedence in eggsac recognition. The artificial eggsacs used in this experiment were smooth, hard, black plastic beads. A normal eggsac of *Pardosa milvina* has a rougher texture, is more pliable, and generally has a hue that ranges from off-white, to tan, to blue. Because artificial eggsacs were chosen less frequently than their own eggsac suggests that these or other eggsac properties such as chemical cues are important in driving eggsac recognition.

Results of the prey capture experiment showed that females carrying an eggsac were significantly less effective in foraging for large crickets than females without an eggsac, but we found no evidence of incremental foraging costs with increasing eggsac weight. Difficulty in prey capture is likely due to decreased locomotor efficiency. For example, females that accepted the 6-mm bead (weighing approximately ten times their own body mass) visibly struggled in transporting an eggsac of such size. Any type of prolonged movement frequently caused the female difficulty in keeping the eggsac attached. Therefore reduced movement likely constrained female success in capturing prey. The 6-mm bead may exceed the size of an eggsac a female *Pardosa* can carry continuously. Although we did not find statistical evidence for incremental foraging costs with size, our results qualitatively match our predictions. Crickets with the longest survival times were in the treatment with *Pardosa* carrying the heaviest eggsacs. There was also a tendency for females to drop larger eggsacs more often than smaller ones while foraging. These eggsacs were not retrieved prior to the end of the experiment, suggesting that losing an eggsac is more likely with increasing mass.

Some previous studies have shown that eggsac-carrying females do not feed and that their predatory behavior is inhibited by carrying an eggsac (Higashi & Rovner, 1975; Foelix, 1996). Our study indicates that this is not necessarily the case among *Pardosa milvina* since between 20 and 60% of encumbered spiders did feed during our experiments. Nyffeler (2000) found 18 instances of female *Pardosa* spp. with eggsacs feeding on prey under field conditions, but noted that these spiders were all feeding on prey much smaller than the prey used in our study and that these females were feeding at a lower rate than unencumbered females. Other studies have found that female body weight remains constant while carrying eggsacs indicating that they likely continue to feed at a regular rate and suffer no reduction in feeding efficiency (Edgar, 1971). Miyashita (1968a,b) however found that female *Pardosa* fed at a lower rate when carrying eggsacs. Lowered feeding rates could be due to adaptive predatory inhibition during maternal care to prevent the female from accidentally consuming her offspring (Wagner, 1995). Our results suggest that reduced feeding rates are simply the result of reduced prey capture efficiency due to carrying eggsacs rather than induced feeding inhibition. Collectively our results combined with these other studies suggest that eggsac-carrying females may restrict their prey preference to smaller prey to minimize the increased difficulty of subjugating prey while simultaneously balancing an eggsac.

We found that females not carrying an eggsac were much more effective at avoiding predation than eggsac-encumbered females. As was the case with foraging, among females with an artificial or real eggsac attached, there were no significant differences in predator avoidance. Interestingly, females carrying the heaviest eggsacs had survival times no different than spiders without eggsacs. One explanation for this observation is that the females with the largest eggsacs showed the least movement. Numerous studies have demonstrated that *Pardosa milvina* are more difficult for *Hogna helluo* to detect when not moving and therefore suffer less predation (Persons et al., 2001, 2002; Barnes et al., 2002; Lehmann et al., 2004).

Females are apparently constrained in terms of prey capture and predator avoidance by the added burden of transporting an eggsac. Previous studies of *Pardosa tristis* have revealed that female spiders carrying weighted eggsacs display changes in both posture and locomotor mechanics (Moffett & Doell, 1980). Females tend to stand with their legs closer together and take shorter steps while carrying weighted eggsacs (Moffett & Doell, 1980). These changes may be responsible for decreased locomotor efficiency that negatively affects both foraging and predator avoidance among females carrying heavier eggsacs.

Although reduced prey capture success and predator avoidance are the most obvious and direct costs of carrying eggsacs, we observed that females occasionally drop their eggsacs during grappling bouts with either prey or predators. The occurrence of this behavior was too infrequent for statistical analysis, but did occur most frequently in the heaviest eggsac treatments. This suggests that females that carry larger eggsacs may be more likely to lose them. It is unknown how common eggsac loss is under natural conditions but there are anecdotal accounts of spiders carrying snail shells on their spinnerets (O'Connor, 1896; Locket & Marsh, 1957). We have also observed rare occasions of females carrying small pebbles, round bits of dirt, and small seeds on their spinnerets (personal observation). Presumably, these present natural cases of mistaken identity equivalent to those induced in our laboratory study. Although not quantitatively measured in our study, search time for dropped eggsacs could present an additional incremental reproductive cost to foraging and predator avoidance based on eggsac size. During anecdotal observations in our lab, females often actively searched for lost eggsacs for up to eight hours.

In both the prey-capture and predator-avoidance experiments there were no significant differences between the 3-mm bead treatment, which was equal in weight to an average eggsac, and the treatment where spiders were carrying their own eggsac. Similarly, in both Pennsylvania foraging and predation experiments there were no significant differences between the 4-mm bead treatment, which was equal in diameter to an average real eggsac, and the own eggsac treatment. Given such substantial differences between a real eggsac and the artificial eggsacs used in this experiment, it is surprising that there were not significant differences between real eggsac treatments, and the 3- and 4-mm bead treatments. This trend suggests that the main properties of eggsacs that contribute to female prey capture of crickets and predator avoidance of larger wolf spiders are mass and volume, rather than texture, hardness, and reduced crypsis due to eggsac coloration.

In providing maternal care, female spiders protect their young from predation and parasitism, drowning, physical damage, temperature fluctuations and fungal attack (Hieber, 1985, 1992). However females may be limited in the number of offspring they can care for without negatively impacting their residual fitness. It is unclear how many eggsacs female *Pardosa milvina* are capable of producing under field conditions, but laboratory-reared females have produced and dispersed spiderlings from up to three viable eggsacs (unpubl. data). These data suggest that females have the physiological ability to produce additional eggs, but may be limited by the mass of the eggsac or subsequent mass of the spiderlings after they exit the eggsac because these are also carried by the female. Our limited data suggest that the foraging and predation costs of carrying eggsacs resemble a step function rather than being incremental.

Acknowledgements

We would like to thank Stacey Brautigam, Katie Sauder, Dianne Rossetti, Ryan Bell, Katrina Waisenen, Jill DeVito, Patrick Sutton, Ann Schlosser and Marlena Koper for help with various aspects of this study. This research was funded in part through NSF grant DBI-0216776 (for M. Persons) and DBI-0216947 (for A. Rypstra).

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