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SPIDER SIZE AND GUARDING OF OFFSPRING AFFECT *PARAPHIDIPPUS AURANTIUS* (ARANEAE, SALTICIDAE) RESPONSE TO PREDATION THREAT

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ABSTRACT. We tested the hypothesis that the response of *Paraphidippus aurantius* (Lucas 1833) (Salticidae) to a simulated threat of predation would depend on a combination of spider size and reproductive status. In ponderosa pine forests of Colorado we located nests with spiders of varying sizes that were either adult female spiders guarding offspring or juvenile female and male spiders. To simulate a predator threat we applied a disturbance to the sides of spider nests using repeated puffs of air expressed from a rubber bulb or by blowing. We recorded the threat intensity (number of puffs) required to displace spiders from their nests, and then monitored the immediate responses of spiders to this threat. The threat intensity required to displace spiders guarding offspring was 2.3 times that of non-guarding spiders, and guarding spiders fled less than half as far as non-guarding spiders. Spider size had no effect on the threat intensity required for displacement, but larger spiders fled further than small ones. We then destroyed nests and monitored the long term responses of the spiders. Nests containing offspring were constructed with 4.6 times the mass of silk as those without offspring. When spiders rebuilt their nests, spider tenure in rebuilt nests did not differ between guarding spiders and non-guarding spiders. Spider size was negatively related to nest tenure for non-guarding spiders, but there was no such relationship for guarding spiders. These results suggest that both the short term and long term outcomes of interactions between *P. aurantius* and other predators may be influenced by a combination of spider size and offspring guarding behavior.

Keywords: Size-structured intraguild predation, parental care, anti-predator strategy

Predators prey not only upon herbivores, but also upon each other in what has been termed intraguild predation (Polis and McCormick 1987; Polis et al. 1989; Polis and Holt 1992; Rosenheim et al. 1995). The predators that have been shown to feed upon spiders include ants (Wise 1993; Halaj et al. 1997; Eubanks 2001; Mooney & Tillberg 2005), birds (Askenmo et al. 1977; Dickson et al. 1979; Gunnarsson 1983; Wise 1993), and other spiders (Pollard 1983; Fink 1987; Austin 1988; Wise 1993). Often intraguild predation is size-structured, whereby the role of predator and prey is determined by the relative mass of the two interacting predators (Werner & Gilliam 1984; Claessen et al. 2002; De Roos et al. 2003). For example, whether *Hogna helluo* (Walckenaer 1837) (Lycosidae) preys upon *Pardosa milvina* (Hentz 1844) (Lycosidae), or vice versa, changes based on which spider is larger at the time of the encounter (Persons & Rypstra 2001).

Models of optimal reproductive behavior predict that a predator's response to the threat of intraguild predation may also shift with changing reproductive status and investment in offspring (Curio et al. 1984; Coleman et al. 1985; Sargent & Gross 1985; Curio 1987; Coleman & Gross 1991). Juveniles may optimize fitness by avoiding potential predators, while adults guarding young or defending nests may optimize their fitness by confronting potential predators and protecting these maternal investments. Maternal protection of eggs and juveniles has been shown in many spiders (Kaston 1948; Eberhard 1974; Matlack & Jennings 1977; Patel & Bradoo 1981; Hoffmaster 1982; Pollard 1983; Fink 1987; Cushing 1989; Hie-

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ber & Uetz 1990; Horel & Gundermann 1992; Gundermann et al. 1997) against threats as diverse as parasitoids, heterospecific predators, conspecific predators, and even pathogenic molds (Pollard 1983; Fink 1986; Austin 1988; Horel & Gundermann 1992; Hieber et al. 2002). The response of spiders to the threat of intraguild predation has been shown to vary based on offspring-protection. Hoffmaster (1982) found that *Philoponella cuminamensis* (Simon 1891) (Uloboridae) without eggs was significantly more likely to drop from their webs when attacked by hummingbirds than those with eggs. Similarly, when *Uloborus glomosus* (Walckenaer 1842) (Uloboridae) was exposed to artificial stimuli by Cushing and Opel (1990), spiders with eggs remained in place longer than those without. Thus the outcomes of intraguild predation may also change based on the reproductive status of the interacting predators.

In the present study we investigated the hypothesis that a spider's response to the threat of a potential predator is likely to vary as a function of both spider size and whether or not the spider is engaged in offspring protection. Using *Paraphidippus aurantius* (Lucas 1833) (Salticidae) as a model organism, we subjected (1) juvenile spiders (small males and females, sex undetermined) and (2) larger, adult females spiders guarding eggs or spiderlings to a simulated threat of predation. We documented both the immediate (time scale of seconds to minutes) and long term (time scale of days to weeks) responses to this threat. Using these data, we identified the separate effects of spider size and reproductive status on behavior, and also whether there was interaction between these effects such that effect of spider size on behavior differed between spiders with and without offspring.

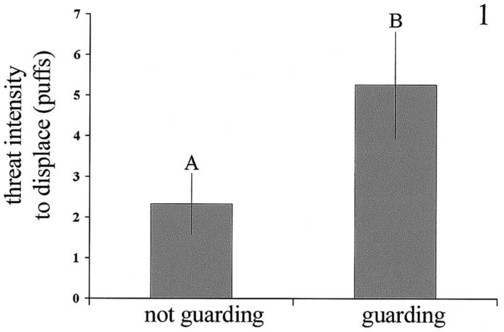
METHODS

This study was conducted at the Manitou Experimental Forest, an administrative unit of the U.S. Department of Agriculture Forest Service Rocky Mountain Experiment Forest in Woodland Park, Colorado USA (39°06′02″N, 105°05″32′W). We worked in mature stands of ponderosa pines (*Pinus ponderosa* Laws. var. *scopulorum*) at an elevation of approximately 2400 m with an understory of herbaceous vegetation and pine saplings.

Paraphidippus aurantius builds small, compact silk nests at the base of pine needle clusters. When these nests are destroyed, *P. aurantius* either rebuilds in the same location or disperses from the sapling (Mooney & Haloin in press). Adult females lay eggs in nests, and spiderlings can remain within or near nests for several days. By late July there are some juveniles, very few adult males, and of the adult females, most have eggs or offspring (Mooney unpubl. data). Thus, the spiders with which we worked were either (1) adult females guarding eggs and spiderlings ('guarding spiders') or (2) male and female juveniles ('non-guarding spiders'). Voucher specimens of *P. aurantius* are deposited at Denver Museum of Nature and Science.

We conducted our first replication of our experiment in 2000. On 22 July we located 22 spiders nesting in saplings and simulated a predator threat by applying force to the nest exterior walls with gentle mouth blowing. We then destroyed each nest, noting whether there were eggs or spiderlings, or whether the nest was empty. In 2001 we conducted a second, modified replication of the experiment. In mid July we located 30 occupied nests. On July 24 we simulated a predator threat by applying force to the nest walls with puffs of air expelled from a rubber bulb at one second intervals, counted the number of puffs required before each spider left its nest, and noted the distance the spider traveled. We visually estimated spider length to the nearest millimeter and collected the nest. Under a dissecting microscope we noted whether there were (1) eggs or spiderlings or (2) whether the nest was empty. We then removed any eggs and spiderlings and weighed the nest silk using a Mettler HK 60 precision balance. In the field we checked for spiders eight times over the next 21 days, specifically on days 1 (one day after nest destruction), 2, 8, 9, 10, 13, 14, and 21. On each visit we noted whether the spider was present and whether it had rebuilt a nest (see Mooney & Haloin in press for information on nest site fidelity).

All analyses were performed using PROC GLM of SAS 6.12 (SAS Institute 1996). Type III sums of squares were used when sample sizes were unbalanced (Zar 1999). Unless otherwise stated, assumptions of normality and heteroskedasticity were met and analyses were performed on untransformed variables.



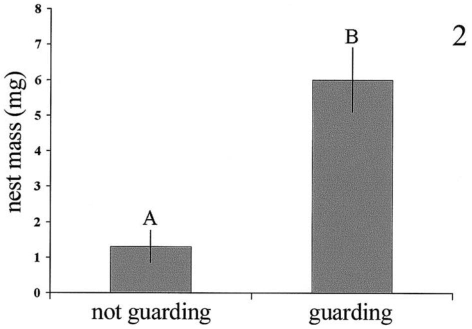


Figure 1.—Mean (± 1 standard error) threat intensity (number of puffs of air) required to displace guarding and non-guarding spiders for spiders tested in 2001. Means differed significantly ($P < 0.05$), as indicated by differing letters above means.

Figure 2.—Mean nest mass (± 1 standard error) for guarding and non-guarding spiders. Means differed significantly ($P < 0.05$), as indicated by differing letters above means.

RESULTS

Of the 30 spiders studied in 2001, 15 were guarding eggs ($n = 6$), spiderlings ($n = 6$), or both ($n = 3$) at the time the experiment was initiated. Brood sizes ranged from 6 to 36 ($n = 13$) with a mean of 18 ± 2.5 (mean ± 1 standard error). Guarding spiders ($n = 15$) were 6 + 2.2 mm in length, while non-guarding spiders ($n = 15$) were 5 ± 2.7 mm and this difference was significant ($F_{(1,28)} = 12.06$, $P = 0.002$).

We tested for effects of spider guarding (a discrete variable) and size (a continuous variable) on the threat intensity required to displace spiders (puffs of air). There was no effect of spider size on threat intensity ($F_{(1,26)} = 1.56$, $P = 0.22$), nor was there interaction between spider guarding and size ($F_{(1,26)} = 1.13$, $P = 0.29$). We dropped spider size from the analysis and a one-way ANOVA showed that threat intensity was significantly higher for guarding than non-guarding spiders. Non-guarding spiders ($n = 15$) required 2 ± 0.8 puffs to be displaced while guarding spiders ($n = 15$), required 5 ± 0.3 puffs ($F_{(1,28)} = 5.02$, $P = 0.033$) (Fig. 1).

The test for an effect of spider guarding and size on empty nest mass (mg silk) suggested no significant relationship between spider size and nest mass ($F_{(1,26)} = 1.60$ $P = 0.22$), nor was there interaction between spider guarding and size ($F_{(1,26)} = 0.14$ $P = 0.71$). We dropped spider size from the analysis and a one-way ANOVA showed that the nests of guarding spiders ($n = 15$) were constructed with 6.0 + 0.9 mg of silk while nests of non-guarding spiders ($n = 15$) weighed only 1.3 ± 0.5 mg and this difference was highly significant ($F_{(1,28)} = 21.53$, $P < 0.0001$) (Fig. 2)

The test for the effects of spider guarding and size on the distance spiders traveled immediately following displacement (linear cm) showed a significant, positive relationship between spider size and travel distance ($F_{(1,26)} = 4.92$ $P = 0.0355$), and there was no interaction between spider guarding and size ($F_{(1,26)} = 0.01$ $P = 0.95$) (Fig. 3). Controlling for spider size, the adjusted mean travel distance for guarding spiders ($n = 15$) was 2.4 cm, while the adjusted mean for non-guarding spiders ($n = 15$) was 5.3 cm, and this difference was significant ($F_{(1,26)} = 8.17$ $P = 0.0083$) (Fig. 3).

To assess whether guarding of offspring affected spider nest rebuilding decisions, we combined data from the 2000 and 2001 disturbance experiments. In total there were 21 guarding and 31 non-guarding spiders. Sixty-two percent (13 spiders) of guarding spiders dispersed from the experimental saplings following our simulated threat of predation, while 48% (15 spiders) of non-guarding spiders dispersed. The number of spiders dispersing did not differ based on offspring guarding ($X_{(3)} = 2.48$, $P = 0.48$). Spiders that rebuilt were 5 ± 0.3 mm in length (mean ± standard error), while spiders that dispersed were 5 ± 0.3 mm and this difference was not significant ($F_{(1,28)} = 0.21$, $P = 0.65$).

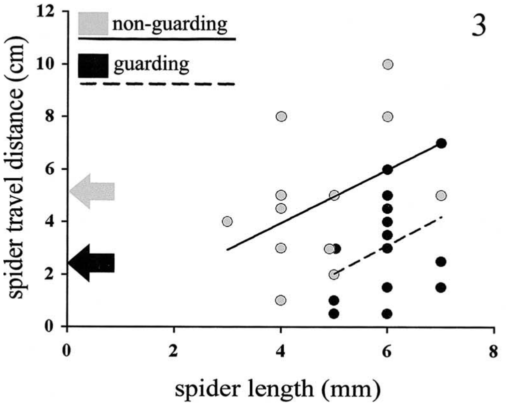
The test for the effects of spider guarding and size on tenure in rebuilt nests showed a trend towards an interaction between spider guarding and size ($F_{(1,26)} = 3.64$, $P = 0.0677$) (Fig. 4). Separate analyses of the relationship between spider size and post-disturbance tenure found no relationship for guarding spiders ($F_{(1,13)} = 0.74$, $P = 0.41$) but a significant, negative relationship for non-guarding spiders ($F_{(1,13)} = 4.67$, $P = 0.0498$). The mean tenure of guarding and non-guarding spiders was 8.8 ± 1.9 days and 7.5 ± 1.9 days respectively, and this difference was not significant ($F_{(1,28)} = 0.24$, $P = 0.63$).

DISCUSSION

There were significant differences between guarding and non-guarding spiders in their immediate responses to our simulated predation threat. Less than half the disturbance intensity was required to displace non-guarding spiders as compared to those guarding offspring. The hesitancy of guarding spiders to flee their nests may not necessarily place them at greater risk of predation because their nests are built with nearly five-times more silk, and this may afford them greater protection from potential predators. Controlling for size, we saw that when spiders did leave their nests, non-guarding spiders fled over twice as far as guarding spiders.

In these comparisons of guarding and non-guarding spiders we did not control for sex or life-stage differences; guarding spiders were adult females while non-guarding spiders were juvenile females and males. However, by controlling for spider size in our comparisons we eliminated at least one important characteristic that differs between adults and juveniles. These results suggest that the outcome of interactions between *P. aurantius* and other predators is likely shaped, in part, by whether or not the spider is a female engaged in offspring guarding behavior.

Spider size did not affect the intensity of disturbance required to displace spiders. When spiders did flee, larger spiders ran further than small ones, contrary to the expectation that larger spiders might remain to confront the challenge. It may be that magnitude of the perceived threat was sufficiently great that all spiders, large and small alike, made the decision to evade the risk, with larger spiders using their relative size advantage to flee further than their smaller conspecifics.



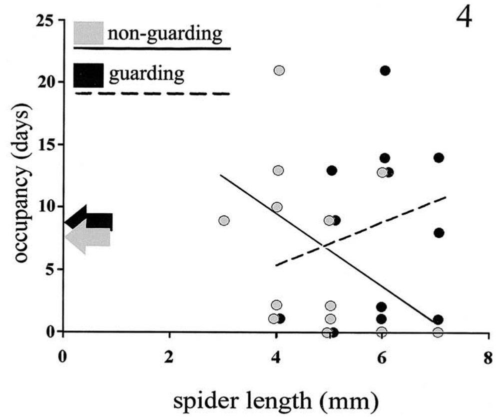


Figure 3.—Relationship between spider length and spider travel distance for guarding spiders (black circles and dashed line) and non-guarding spiders (shaded circles and solid line). The mean spider travel distance for both groups, adjusted for spider length, are shown with black and shaded arrows respectively, and differed significantly ($P < 0.05$).

Figure 4.—Relationship between spider length and occupancy tenure of rebuilt nests for guarding spiders (black circle and dashed line) and non-guarding spiders (shaded circles and solid line). Spider size was negatively related to nest occupancy for non-guarding spiders ($P = 0.0498$). There was no such relationship for guarding spiders ($P = 0.41$). The interaction between guarding and size was close to significant ($P = 0.0677$). The mean post-disturbance tenures of guarding and non-guarding spiders are shown with black and grey arrows respectively.

Neither spider guarding nor size affected the decision of whether to rebuild the nest or to disperse. For non-guarding spiders, small spiders occupied rebuilt nests longer than larger ones. There was no such relationship between spider size and guarding spiders. Dispersion likely carries greater risks for smaller spiders, and this risk seems to be reflected in the decisions of non-guarding spiders. Egg laying may change risk-avoidance decisions such that for guarding spiders, size is of less important than offspring guarding in the decision of when to disperse. Other work has shown that the reproductive status significantly alters spider behaviors (Horel & Gundermann 1992; Bessekon & Horel 1996).

Intraguild predation is interesting because often either of the two interacting predators can become predator or prey. Our work suggests that outcome of predator-predator interactions are likely to be structured by both the size and reproductive status of the predators. Furthermore, we have presented evidence that predator sizes and reproductive status may interact, such that the nature of size-structured interactions may depend on whether or not the predators are engaged in offspring guarding behaviors.

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