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
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; Pink 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.
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 ($X^2_{(3)} = 2.48, P = 0.48$). 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.
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 importance 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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LITERATURE CITED

Askenmo, C., A.V. Bromssen, J. Ekman & C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos 28:90–94.

Austin, A.D. 1988. Guarding behavior, eggmass shape and the egg sac in *Clubiona robusta* L. Koch (Araneae: Clubionidae). Pages 87–95. In A. D. Austin and N. W. Heather, editors. Australian Arachnology. The Australian Entomological Society, Brisbane, Australia.

Bessekon, D.A., & A. Horel. 1996. Social-maternal relations in *Coelotes terrestris* (Araneae, Agelenidae): Influence of the female reproductive state on its tolerance towards conspecific spiderlings. Behavioural Processes 36:19–25.

Claessen, D., C. Van Oss, A.M. De Roos & L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology 83:1660–1675.

Coleman, R.M. & M.R. Gross. 1991. Parental investment theory—the role of past investment. Trends in Ecology & Evolution 6:404–406.

Coleman, R.M., M.R. Gross & R.C. Sargent. 1985. Parental investment decision rules—a test in bluegill sunfish. Behavioral Ecology and Sociobiology 18:59–66.

Curio, E. 1987. Animal decision-making and the conceerde fallacy. Trends in Ecology & Evolution 2:148–152.

De Roos, A.M., L. Persson & E. McCauley. 2003. The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. Ecology Letters 6:473–487.

Dickson, J.G., R.N. Conner, R.R. Fleet, J.C. Kroll & J.A. Jackson. 1979. The Role Of Insectivorous Birds In Forest Ecosystems. Academic Press, New York.

Eberhard, W.G. 1974. Maternal behavior in a South American *Lyssomanes*. Bulletin of the British Arachnological Society 3:51.

Eubanks, M.D. 2001. Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. Biological Control 21:35–43.

Fink, L.S. 1986. Costs and benefits of maternal behavior in the green lynx spider (*Oxyopidae, Peucetia viridans*). Animal Behaviour 34:1051–1060.

Fink, L.S. 1987. Green lynx spider egg sacs—sources of mortality and the function of female guarding (Araneae, Oxyopidae). Journal of Arachnology 15:231–239.

Gundermann, J.L., A. Horel & C. Roland. 1997. Costs and benefits of maternal care in a subsocial...
spider, *Coelotes terrestris*. Ethology 103:915–925.

Gunnarsson, B. 1983. Winter mortality of spruce-living spiders—effect of spider interactions and bird predation. Oikos 40:226–233.

Halaj, J., D.W. Ross & A.R. Moldenke. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. Oecologia 109:313–322.

Hieber, C.S. & G.W. Uetz. 1990. Colony size and parasitoid load in two species of colonial *Metepeira* spiders from Mexico (Araneae, Araneidae). Oecologia 82:145–150.

Hieber, C.S., R.S. Wilcox, J. Boyle & G.W. Uetz. 2002. The spider and fly revisited: ploy-counterploy behavior in a unique predator-prey system. Behavioral Ecology and Sociobiology 53:51–60.

Hoffmaster, D.K. 1982. Predator avoidance behaviors of five species of Panamanian orb-weaving spiders (Araneae, Araneidae, Uloboridae). Journal of Arachnology 10:69–73.

Horel, A. & J.L. Gundermann. 1992. Egg sac guarding by the funnel-web spider *Coelotes terrestris*—function and development. Behavioural Processes 27:85–93.

Kaston, B.J. 1948. Spiders of Connecticut. Connecticut State Geological and Natural History Survey Bulletin. 874 pp.

Matlack, M.C. & D.T. Jennings. 1977. Cobhabitation of female spiders guarding egg sacs. Journal of the Kansas Entomological Society 50:519–522.

Mooney, K.A. & J.R. Haloin. In press. Nest site fidelity of *Paraphidippus aurantius* (Salticidae). Journal of Arachnology.

Mooney, K.A. & C.V. Tillberg. 2005. Temporal and spatial variation of ant omnivory in pine forests. Ecology 86(5):1225–1235.

Patel, B.H. & B.L. Bradoo. 1981. The cocoon spinning behavior and maternal care in *Uloborus ferokus* Bradoo (Araneae: Uloboridae). Zoologischer Anzeiger, Jena 207:78–87.

Persons, M.H. & A.L. Rypstra. 2001. Wolf spiders show graded antipredator behavior in the presence of chemical cues from different sized predators. Journal of Chemical Ecology 27:2493–2504.

Polis, G.A. & R.D. Holt. 1992. Intraguild predation—the dynamics of complex trophic interactions. Trends in Ecology & Evolution 7:151–154.

Polis, G.A. & S.J. McCormick. 1987. Intraguild predation and competition among desert scorpions. Ecology 68:332–343.

Polis, G.A., C.A. Myers & R.D. Holt. 1989. The ecology and evolution of intraguild predation—potential competitors that eat each other. Annual Review of Ecology and Systematics 20:297–330.

Pollard, S.D. 1983. Egg guarding by *Clubiona cambridgei* (Araneae, Clubionidae) against conspecific predators. Journal of Arachnology 11:323–326.

Rosenheim, J.A., H.K. Kaya, L.E. Ehler, J.J. Marois & B.A. Jaffee. 1995. Intraguild predation among biological-control agents—theory and evidence. Biological Control 5:303–335.

Sargent, R.C., & M.R. Gross. 1985. Parental investment decision rules and the concorde fallacy. Behavioral Ecology and Sociobiology 17:43–45.

SAS Institute. 1996. SAS version 6.12. SAS Institute, Cary, N.C.

Schmitz, O.J., ER. Adler & A.A. Agrawal. 2003. Linking individual-scale trait plasticity to community dynamics. Ecology 84:1081–1082.

Werner, E.E. & J.F. Gilliam. 1984. The Ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics 15:393–425.

Wise, D.H. 1993. Spiders In Ecological Webs. Cambridge University Press, Cambridge ; New York. 328 pp.

Zar, J. H. 1999. Biostatistical Analysis, 4th edition. Prentice Hall, Upper Saddle River, N.J. 663 pp.

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