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SIZE DEPENDENT INTRAGUILD PREDATION AND CANNIBALISM IN COEXISTING WOLF SPIDERS (ARANEAE, LYCOSIDAE)

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ABSTRACT. Two species of wolf spider, *Hogna helluo* (Walckenaer 1837) and *Pardosa milvina* Hentz 1844 dominate the predatory community on the soil surface of agroecosystems in eastern North America. Although as adults they are very different in size, differences in phenology ensure that they overlap in size at various times during the year. In a laboratory experiment, we explored the propensity of each species to attack and kill the other wolf spider species (intraguild predation), conspecifics (cannibalism) or crickets (ordinary predation). Both spiders attacked and killed a broader size range of crickets more quickly than they approached other spiders. We found no differences in *Hogna* foraging on conspecifics or *Pardosa*, but *Pardosa* attacked and killed *Hogna* more readily than conspecifics. Because *Hogna* was so slow in attacking other spiders, their impact as an intraguild predator may be quite small, especially if their approach to crickets is an indication of their predatory tendencies with insects. On the other hand, *Pardosa* attacked and killed small *Hogna* as readily as crickets, which suggests they may have an influence on *Hogna* populations if *Hogna* young emerge coincident with large juvenile or adult *Pardosa*.

Keywords: Cannibalism, intraguild predation, agrobiont spiders, predator-prey

Cannibalism and intraguild predation (IGP) are important to spider communities and have the potential to affect population sizes and/or species diversity of spiders as well as that of potential insect prey (Wagner & Wise 1996; Hodge 1999; Samu et al. 1999; Finke & Denno 2002; Matasumura et al. 2004; Denno et al. 2004). Predation is a dynamic process, the outcome of which depends on the relative sizes of the predator and prey, their physiological state, attack strategy and inherent aggressiveness (Walker et al. 1999; Persons et al. 2001; Buddle 2002; Balfour et al. 2003; Buddle et al. 2003; Mayntz et al. 2005). Many of these factors will shift over time both with age and recent experience and thus the relative importance of cannibalism and/or IGP to foraging individuals, population structure and community composition will shift as well (Wagner & Wise 1996; Balfour et al. 2003; Buddle et al. 2003). For spiders that coexist, an understanding of the situations under which cannibalism and IGP occur is critical to understanding how and when they can persist in the same habitat.

In the present study we explore the predatory tendencies of two species of wolf spider (Araneae, Lycosidae) that coexist on the soil surface in agricultural fields across the eastern portion of North America. Because the species differ in size, activity, and phenology, we wanted to characterize the circumstances under which these spiders engaged in cannibalism or intraguild predation and compare those predatory interactions to attacks on insect prey. Under controlled laboratory conditions, we paired a wide size range of individuals with conspecifics, the other species of spider, or crickets and documented the outcome and timing of predation. In this way, we hoped to gain a better understanding of the specific predatory strategy of each of the spider species and the relative influence that these species have on their insect prey, which would help us to gain insight into the nature of their co-existence.

METHODS

Study species.—*Hogna helluo* (Walckenaer 1837) and *Pardosa milvina* Hentz 1844 coexist on the soil surface in disturbed riparian habitats and agroecosystems throughout the

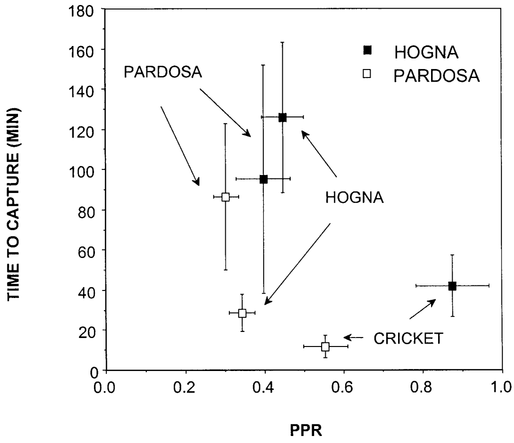

Figure 1.—Mean prey to predator mass ratio (PPR ± S.E.) for captured prey vs. the time (min ± S.E.) it took the prey to be captured. Trials where *Hogna* was predator are indicated by solid squares and those where *Pardosa* was predator are indicated by open squares. Specific prey types are listed with an arrow pointing to the data for that treatment.

eastern portion of North America (Dondale & Redner 1990; Marshall & Rypstra 1999; Marshall et al. 2002). *Pardosa* is small (20 mg), active, and can be found at high densities (10–15 per m^2) whereas *Hogna* is large (800 mg), less active, and found at relatively low densities (1–2 per m^2) in soybean fields in the midwestern section of the United States (Marshall & Rypstra 1999; Walker et al. 1999; Marshall et al. 2002). *Pardosa* is an annual species with a mid-July population peak. Except for a relatively short period during which the adults and spiderlings co-occur, the size distribution of *Pardosa* individuals active in the fields at any given time is fairly narrow (Marshall et al. 2002). On the other hand, *Hogna* seems to have a two-year life cycle with more stages occurring in the fields at the same time (Marshall et al. 2002). Although *Hogna* are usually larger than *Pardosa*, because of the variability in their life cycle, it is possible for large subadult or adult *Pardosa* to coexist with early stages of *Hogna*. Previous studies have revealed that each species readily consumes smaller individuals of the other in the laboratory (Persons et al. 2001; Balfour et al. 2003). Here we explore those predatory interactions systematically across a broad range of size ratios.

Both species of spiders were collected from corn and soybean fields at the Miami University Ecology Research Center (Oxford, Butler County, Ohio, USA) and held in the laboratory or reared from animals collected at that site. When not involved in experimentation, spiders were housed individually in translucent plastic cylindrical containers 8 cm in diameter with 5 cm walls with 1–2 cm of damp peat moss covering the bottom. Spiders were watered and fed once or twice weekly on a diet of crickets (*Acheta domesticus*), fruit flies (*Drosophila* spp.) and or meal worms (*Tenebrio* spp.). Containers with spiders were held in an environmental chamber between 23—25 °C on a 12:12 L:D cycle at 60–75% humidity.

Experimental protocol.—Spiders were randomly selected from the laboratory population and brought to standard hunger levels by feeding them *ad libitum* with *Drosophila melanogaster* for 2 days. Spiders were then held for 7 days before testing to ensure that they were similarly hungry. Spiders were randomly assigned to be paired with conspecifics (to monitor cannibalism), heterospecifics (to monitor intraguild predation) or crickets (to monitor ordinary predation). Those assigned to be paired with conspecifics were marked with a drop of acrylic paint on the abdomen or cephalothorax so that we could identify individuals. All spiders and crickets were weighed and then introduced into a testing arena simultaneously. The arenas consisted of 14 cm diameter Petri dishes with a base of dampened plaster of Paris (as in Samu et al. 1999). Animals were allowed to interact in the arena for 24 h during which time we recorded if and when predation occurred. Experiments were run in groups that included representatives of all treatments between July 1998 and July 2001.

Statistical analysis.—In order to determine how similar the spiders and insects used in each treatment were, we compared the mass of predators and prey across all treatments in ANOVAs. In addition, we calculated prey/predator mass ratio (PPR) by dividing the mass of the prey by the mass of the predator. In cases where there was no predation, we randomly assigned one of the spiders as prey and the other as predator using a coin toss algorithm. In order to ensure pairings were similar across treatments, PPRs were also compared in an ANOVA. The effects of predator species, prey type, and PPR on the frequency of predation were compared using a

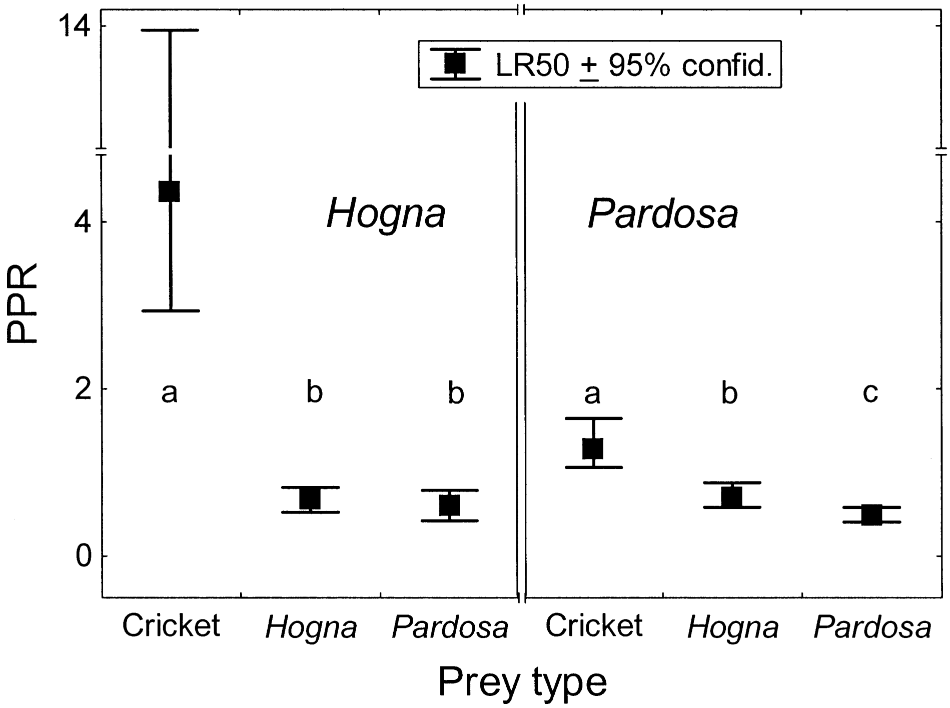

Figure 2.—Fifty percent lethal mass ratio (LR50) (± 95% confidence interval) for *Hogna* (on the left) and *Pardosa* (on the right). Prey type is on the X-axis. Where treatments are indicated with the same small letter in the middle of each figure, the overlap of the 95% confidence ranges suggests that there was no significant difference.

logistic regression analysis. From the logistic regression, we determined the PPR at which there was a 50% likelihood of a predatory event (LR50). Differences in LR50s across treatments were evaluated by comparison of the 95% confidence intervals. The effects of the same factors (predator species, prey type, and PPR) on the time until predation were evaluated using a parametric survival analysis using the Proportional Hazards model. In this case pairwise comparisons were made using the Bonferroni test with an overall P-value of 0.05. Both the logistic regression and survival models were run initially with all interactions included. The non-significant interactions were removed after the first run and the models were run again.

We also wanted to determine if any of the observed preferences were due to size or if they had to be attributed to some other quality of the prey (e.g. nutrition, taste). We hypothesized that, if the preference was size related, then there would be a size ratio ($PPR_{critical}$) below which predators would not discriminate between prey types. We defined $PPR_{critical}$ as the maximum PPR value where the differences between predation on two prey types were no longer significantly different ($P = 0.05$). In order to find the $PPR_{critical}$, we started by removing the sample with the highest PPR and rerunning the statistical test, if it was still significant, we removed the sample with the next highest PPR, and ran the test again. We continued this process until the P-value associated with any difference was equal to 0.05.

RESULTS

Overall there were no differences in the mass of the *Hogna, Pardosa,* or crickets used in our treatments (Predator mass F = 1.81, df = 5, 401, $P = 0.11$; Prey mass F = 1.02, df = 5, 401, $P = 0.40$) (Table 1). In addition, animals were paired so that the PPR values were similar across treatments (F = 1.71, df = 5, 401, $P = 0.13$) (Table 1). Even though not significantly different, the PPR for *Hogna* on crickets was somewhat higher than the oth-

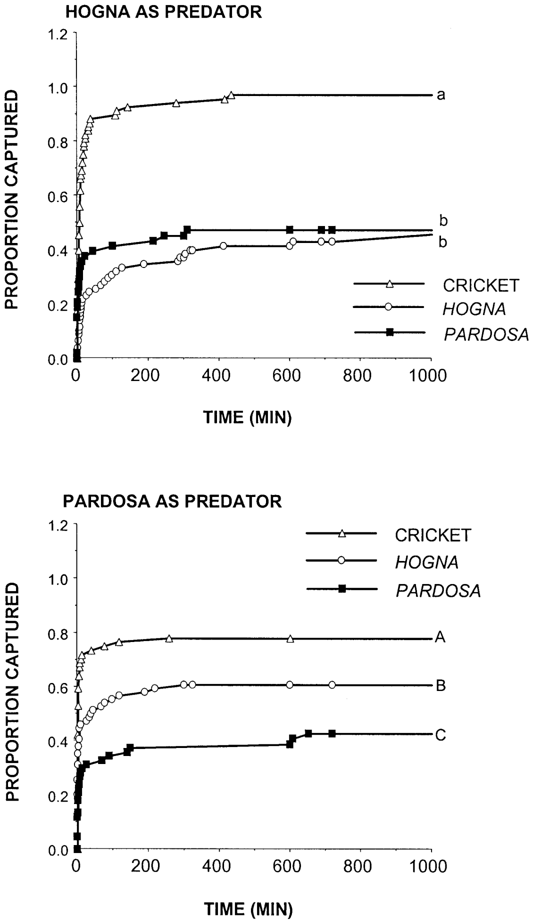

Figure 3.—Capture success over time of *Hogna* and *Pardosa* on the three different prey types. Those indicated with the same letter (at the right of the line) were not significantly different using Bonferroni comparisons with a critical value of 0.05.

ers. To some degree, this variation was intentional as we attempted to observe interactions across the complete prey size range that each spider would take. Note that even though the PPR is close to one, meaning that the prey were the same size as the predator, the capture rate is still very high (94.3%) as compared to other treatments (Table 1). Predator species, prey species and the PPR all affected the occurrence and the timing of predation in complex ways (Table 2).

Predation on crickets vs. spider prey.—Both *Hogna* and *Pardosa* had higher capture success on crickets than on spiders (*Pardosa*: $\chi^2_{195} = 10.19$, $P = 0.001$; *Hogna*: $\chi^2_{209} = 54.54$, $P < 0.0001$; Table 1). Both species killed larger crickets than they killed other spiders (higher PPR) (Fig. 1). However at PPRs less than 0.54 for *Pardosa* ($\mathrm{PPR}_{\mathrm{critical}}$, $\chi^2_{97} = 3.82$, $P = 0.05$) and 0.57 for *Hogna* ($\mathrm{PPR}_{\mathrm{critical}}$, $\chi^2_{74} = 3.46$, $P = 0.05$) there were no differences between spider vs. cricket prey. The process by which we generated the $\mathrm{PPR}_{\mathrm{critical}}$ inevitably resulted in a loss of sample size, and therefore power, however, we regard the remaining case numbers still large enough ($N_{\mathrm{Pardosa}} = 98$, $N_{\mathrm{Hogna}} = 75$) to draw valid conclusions on $\mathrm{PPR}_{\mathrm{critical}}$ values. The PPR at which there was a 50% chance of a predatory event (LR50) was significantly higher for crickets than for spider prey (Fig. 2). Likewise, overall crickets were killed more quickly than other spiders (Figs. 1, 3).

Comparing the predation strategy of *Hogna* and *Pardosa*.—The two predators differed in their responses to the prey types tested (Table 2). *Hogna* consistently took larger prey than *Pardosa* from every prey category (Figs. 1, 2). On the other hand, *Pardosa* was consistently faster than *Hogna* in taking every prey type (Figs. 1, 3). *Pardosa* was more likely to capture *Hogna* than conspecifics ($\chi^2_{139} = 5.53$, $P = 0.018$, Table 1) but there was no difference in the capture rate of *Hogna* on either spider species ($\chi^2_{131} = 0.27$, NS; Table 1). Likewise, the LR50 was larger for *Pardosa* preying on *Hogna* than it was for *Pardosa* cannibalism (Fig. 2) but there was no difference in the LR50 for *Hogna* preying on heterospecifics or conspecifics (Fig. 2). Similarly *Pardosa* captured *Hogna* more quickly than it captured other *Pardosa* but there were no differences in the *Hogna*'s predatory speed on conspecifics or heterospecific spiders (Figs. 1, 3).

DISCUSSION

Clearly these two spider species, *Hogna helluo* and *Pardosa milvina,* differ in their foraging behavior across the various sizes of the different prey types tested here. *Hogna* is generally slower to attack and kill a potential prey but generally take prey in larger size classes than *Pardosa*. Although *Hogna* differentiated between crickets and spiders, they did not seem to differentiate between conspecifics and a common coexisting intraguild predator, *Pardosa*. On the other hand, *Pardosa* reacted differently to all three prey types; killing larger crickets faster than they killed *Hogna* and kill-

Table 1.—Summary of the sample size, capture frequency, predator mass (±S.E.), prey mass (±S.E.), and prey to predator mass ratio (PPR ± S.E.) for each treatment.

Treatments	*n*	Number captured (%)	Predator mass (mg)	Prey mass (mg)	PPR
Hogna on crickets	70	66 (94.3%)	14.4 ± 1.2	14.6 ± 1.9	0.97 ± 0.11
Hogna on *Hogna*	78	34 (43.6%)	19.2 ± 1.2	11.7 ± 1.7	0.84 ± 0.07
Hogna on *Pardosa*	54	28 (48.1%)	19.5 ± 1.4	9.9 ± 2.1	0.63 ± 0.05
Pardosa on crickets	64	50 (78.1%)	19.6 ± 1.3	11.1 ± 1.8	0.75 ± 0.07
Pardosa on *Hogna*	74	44 (59.5%)	17.6 ± 1.2	9.2 ± 1.8	0.64 ± 0.06
Pardosa on *Pardosa*	66	38 (42.4%)	19.1 ± 1.3	12.2 ± 1.9	0.68 ± 0.06
All Groups	406	260 (64.1%)	18.4 ± 1.6	11.4 ± 2.1	0.76 ± 0.03

ing larger *Hogna* faster than they killed conspecifics.

Predation on crickets vs. spider prey.—Both cannibalism and IGP have been extensively documented in wolf spiders (Wagner & Wise 1996; Samu et al. 1999; Balfour et al. 2003; Buddle et al. 2003). Because these interactions carry with them an increased risk of injury and/or reciprocal predation, we expected a different, and perhaps more cautious, predatory approach to other spiders when compared to crickets. We reasoned that the relative size of the prey to its predator (PPR) would be one measure of risk and we found that the PPR at which there was a 50% chance of a predatory event was much higher for crickets than spider prey (Fig. 2). However further exploration of the data reveals that, for both spider species, there was a $\mathrm{PPR}_{\mathrm{critical}}$ below which there were no differences in the rate of predation on spiders as compared to crickets. Thus, the significant differences in predatory strategy that we observed were due to behavioral shifts that occurred when the prey were large relative to the predator. These results confirm that relative size was more important for spider on spider contests than for attacks of crickets and suggests that both spider species were sensitive to the risk that a large predatory prey item might pose. This connection may be particularly true for *Hogna*, which easily subdued large crickets but were much slower to take smaller individuals of either spider species (Fig. 2).

Even though risk may be important to the observed differences in predation frequency, there may be other reasons for spiders to prefer insect over spider prey. It has been argued that organisms feeding on the same trophic level, and especially conspecifics, provide nutrients in proportions that are more closely aligned with the predator's nutritional needs (Polis 1981; Wildy et al. 1998; Fagan et al. 2002), however several studies have demonstrated that growth and survival of wolf spiders is lower when maintained on spider diets than when provided with insect prey (Toft & Wise 1999; Oelbermann & Scheu 2002; Matsumura et al. 2004). Another reason not to eat closely related species is that they may carry pathogens that can invade more easily when consumed by a conspecific or phylogenetically close host (Pfennig, et al. 1998; Pfennig 2000; MacNeil et al. 2003). Thus, selection may favor preferences for non-spider prey.

Of course wolf spiders behave differently from crickets, which may have reduced their susceptibility to capture. We attempted to control the circumstances of the interaction so that the predator had access to the same kind of sensory information in a confined space, which should minimize the small differences in capture and escape tactics. Nevertheless, it is impossible to totally uncouple the prey preferences and ease of capture from the specific signals by which the predator detects and identifies prey items (Uetz 2000; Uetz & Roberts 2002). Thus a further exploration of the role of specific sensory modalities in the predator interactions of these species is warranted.

Comparing the predation strategy of *Hogna* and *Pardosa*.—A variety of differences between the foraging strategies of *Pardosa* and *Hogna* have been documented (Walker et al. 1999; Walker & Rypstra 2002) and this study clarifies some additional aspects of those differences. In particular, although *Hogna* was the most effective predator on crickets, *Pardosa* distinguished between the three prey types in the proportion (Table 1), size (Figs.

Table 2.—Results of logistic regression to predict prey capture and the results of the proportional hazards survival model to predict the time it took the spiders to capture prey. Both models used predator species, prey species and prey to predator mass ratio (PPR) as predictors.

Source	df	Chi squared	*P*
Logistic regression model for outcome			
Whole model	7	299.782	<0.0001
Predator species	1	9.333	0.0023
Prey species	2	66.809	<0.0001
PPR	1	82.225	<0.0001
PPR * predator	1	20.895	<0.0001
PPR * prey	2	21.807	<0.0001
Survival model for time until capture			
Whole model	9	401.4444	<0.0001
Predator species	1	8.534	0.0035
Prey species	2	189.060	<0.0001
PPR	1	302.410	<0.0001
PPR * predator	1	36.730	<0.0001
PPR * prey	2	85.380	<0.0001
Predator * prey	2	14.433	0.0007

1, 2) and timing (Figs. 1, 3) of predation. *Pardosa* is a much more active species than *Hogna* (Walker et al. 1999; Walker & Rypstra 2002), which might have caused us to predict that they would be more susceptible to predation by other wolf spiders which use motion to detect prey (Persons & Uetz 1997). However, there is no evidence here to demonstrate that activity made *Pardosa* any more susceptible to the sit and wait predator, *Hogna*. In fact, it appears here that activity translated into effective search behavior that increased *Pardosa*'s ability to detect and attack more sluggish arthropod prey such as *Hogna*.

Although not significantly different, the PPRs for *Hogna* paired with crickets were somewhat higher than the other pairings because of our desire to cover the full size range of prey that each spider would attack. Thus we considered whether the longer capture times observed for *Hogna* on crickets (Fig. 1) might be due primarily to the fact that they were tested with larger prey items. However, if we compare the mean capture time for crickets larger than the *Hogna* (PPR > 1.0; $n = 19$) with the capture times for those prey smaller than the *Hogna* (PPR < 1.0; $n = 51$), there was no difference ($t = 2.0$, $P = 0.24$). This fact furthers the characterization of *Hogna* as a slow selective predator that, in the context of the options offered here, prefers large harmless prey. On the other hand, *Pardosa* was generally faster to attack and discriminated more finely between the three prey options we included in this study.

Implications for species co-existence in the field.—These results may be especially important for agrobiont spiders, such as *Hogna* and *Pardosa*, as they may be important agents of biological control. The fact that crickets were more susceptible to predation across a much larger size range than spider prey suggests that the influence that two wolf spider species have on one another may not be exceedingly strong when alternative insect prey are abundant. To fully assess the field importance of these interactions, our findings need to be interpreted in the context of the life history of natural populations. Unfortunately, in spite of existing field surveys (Marshall & Rypstra 1999; Marshall et al. 2002), the life histories of the two species seem to be highly variable and, as a result, are not well enough understood to be predictable. Nevertheless, the available data suggest that *Hogna* typically has a two or three-year life cycle with several juvenile stages coexisting and *Pardosa* is an annual species with a narrower size distribution at any given time in the season. Thus, all life stages of *Pardosa* have the potential of coexisting with larger *Hogna* whereas only when *Hogna* spiderlings emerge at times of the year when large juveniles and adult *Pardosa* are around, do *Hogna* face predation risk from *Pardosa*. Although the trials suggest that *Hogna* exert modest predatory pressure on both conspecifics and *Pardosa*, their attacks were very slow (Figs. 1, 3). As a consequence, *Hogna* may not exert much predation pressure on a quick wolf spider like *Pardosa* that in an open field situation could run away. On the other hand, *Pardosa* appear to prey on small *Hogna* as quickly as on crickets, so *Hogna* that emerge and attempt to go through the first few instars during the early summer, when *Pardosa* are adults, maybe severely impacted by *Pardosa* predation. Clearly further explorations of the interactions between these two species in more natural situations are required to fully quantify their influence on one another, the nature of their coexistence and their potential role in the ecosystem.

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