

WOLF SPIDERS SHOW GRADED ANTIPREDATOR BEHAVIOR IN THE PRESENCE OF CHEMICAL CUES FROM DIFFERENT SIZED PREDATORS

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(Received March 26, 2001; accepted July 25, 2001)

Abstract—The wolf spider, *Pardosa milvina*, displays effective antipredator behavior (reduced activity) in the presence of silk and excreta cues from adults of another cooccurring wolf spider, *Hogna helluo*. However, *Pardosa* and *Hogna* engage in size-structured intraguild predation, where *Pardosa* may be either the prey or predator of *Hogna*. We tested the ability of adult female *Pardosa* to vary antipredator responses toward kairomones produced by *Hogna* that vary in size. *Hogna* were maintained on filter paper for 24 hr. We then presented the paper to adult female *Pardosa* simultaneously paired with a blank sheet of paper. One treatment had two sheets of blank paper to serve as a control. The *Hogna* stimulus treatments were as follows ($N = 15/\text{treatment}$): (1) 1 *Hogna* half the mass of *Pardosa*; (2) 1 *Hogna* of equal mass of a *Pardosa*; (3) 1 adult *Hogna*, 30 times the mass of *Pardosa*; and (4) 8 *Hogna* each 0.25 the mass of *Pardosa*. *Pardosa* decreased activity in the presence of kairomones from *Hogna* of equal or larger size, but showed no change in activity in the presence of a blank control or from a single *Hogna* smaller than itself. *Pardosa* showed a reduction in activity in the presence of cues from eight small *Hogna*. *Pardosa* avoided substrates with adult *Hogna* cues, but showed no avoidance response to any other treatment. These results suggest that *Pardosa* is showing graded antipredator behavior relative to the quantity of predator kairomones present rather than directly discriminating among the different sizes of the predator.

Key Words—*Pardosa milvina*, Lycosidae, kairomone, wolf spider, predator, size, *Hogna helluo*, antipredator, size discrimination, chemical cue.

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INTRODUCTION

Many animals show defensive behavior in the presence of chemical cues produced by predators (see Kats and Dill, 1998, for a review). Antipredator responses include reduced locomotion, increased cover-seeking, or increased vigilance (reviewed in Lima and Dill, 1990; Lima, 1998). These behaviors are generally costly because they interfere with both foraging (Lima and Dill, 1990) and reproduction (Forsgren, 1992; Berglund, 1993; Hedrick and Dill, 1993; Godin, 1995). The "threat-sensitive predator avoidance" hypothesis suggests that prey should show graded responses of defensive behavior proportional to the perceived risk (Dill and Fraser, 1997; Sih, 1997; Puttlitz et al., 1999).

Prey that respond to chemical cues from predators (kairomones) rather than using other sensory cues may overestimate predation risk by exhibiting antipredator behavior even in the absence of the predator itself. This additional cost may be reduced by extracting more information about predation risk from predator cues. Variation in the composition of predator excreta may provide information about the predator's diet (Crowl and Covich, 1990; Chivers et al., 1996; Murray and Jenkins, 1999; Venzon et al., 2000; Persons et al., 2001), which, in turn, may provide information about the proclivity of a predator to feed on particular prey types (Punzo and Kukoyi, 1997; Persons and Rypstra, 2000). Other features such as age or type of chemical cue also may provide information about how recently a predator was in the area (Venzon et al., 2000) as well as the kind of predator present. In some cases, the intensity of kairomone-mediated antipredator responses may be related to the relative size of the prey compared to the predator. For example, dragonfly larvae are effective predators of small tadpoles, but are less efficient preying on tadpoles of larger sizes (Caldwell et al., 1980). Toad tadpoles show a corresponding reduction in antipredator behavior when detecting kairomones from dragonfly larvae as tadpole size increases (Laurila et al., 1997). Collectively, these sources of information may provide animals with a more accurate assessment of predation risk and allow them to modify defensive behavior, mitigating some of the costs of antipredatory behavior.

The wolf spiders *Hogna helluo* and *Pardosa milvina* are among the most abundant ground predators in agricultural fields of the midwestern United States (Marshall and Rypstra, 1999). These two species exhibit size-structured intraguild predation, whereby the role of predator and prey is determined by the relative mass of each spider during an encounter. Adult *Hogna* are typically 20–30 times the body mass of an adult *Pardosa* and are more likely to be the predator during an interspecific encounter, yet we have observed adult *Pardosa* feeding on juvenile *Hogna* as well as adult *Hogna* feeding on adult *Pardosa*. *Pardosa* may benefit from the ability to perceive relative *Hogna* size through kairomone cues since predation risk increases with increasing asymmetry in size (Samu et al., 1999). Adult female *Pardosa* exhibit reduced speed and frequency of movement in the presence of

excreta and silk from adult *Hogna* (Persons et al., 2001). Adult female *Pardosa* also will avoid substrates containing cues from adult *Hogna* when given a choice. These responses are absent when *Pardosa* are presented silk and excreta from conspecifics (Persons et al., 2001). Reduced activity results in longer periods of time in areas with predator cues; however, such behavior is adaptive since slower movement and inactivity increases survival of *Pardosa* in the presence of *Hogna* (Persons et al., 2001).

Pardosa and *Hogna* provide an opportunity to test the threat-sensitive predator avoidance hypothesis. Adults of the smaller *Pardosa* should closely match antipredator response with predation risk. *Pardosa* that interpret chemical cues from a small *Hogna* as a potential predator will incur a number of unnecessary costs. Reduced activity may impair reproductive behavior and may also impair feeding efficiency by causing the spider to avoid a potential prey item. If *Pardosa* can match defensive behavior with relative risk by assessing predator size indirectly, then the spider may minimize the associated costs of defensive behavior. It is unknown if silk and excreta change qualitatively or quantitatively with spider size or if *Pardosa* is able to detect such differences. Here, we test several predictions related to the ability of *Pardosa* to perceive *Hogna* size based on chemical information. First, adult female *Pardosa* will show decreasing activity in the presence of chemical cues from *Hogna* of increasing size, but will show no reduction in activity in the presence of chemical cues from *Hogna* smaller than *Pardosa*. Second, adult female *Pardosa* will not reduce activity in the presence of large quantities of chemical cues from many *Hogna* each smaller than itself. Third, when given a choice, *Pardosa* will avoid silk and excreta produced by *Hogna* larger than itself, but show no avoidance of cues produced by smaller *Hogna*.

METHODS AND MATERIALS

Spider Collection and Maintenance. Spider maintenance, experimental design, and testing protocols are similar to those found in Persons et al. (2001). Seventy-five adult female *Pardosa* were collected from within and along the margins of soybean fields (Oxford, Ohio, Butler County, Ecology Research Center, Miami University) in September 1998. *Pardosa* used as test spiders were fed a meal of two domestic cricket nymphs (*Acheta domesticus*) once a week followed by five additional cricket nymphs one day prior to testing to minimize possible hunger effects on activity. All spiders were maintained in 8-cm-diam. \times 5-cm-high plastic translucent containers lined with moistened peat moss and kept in environmental chambers on a 13L:11D light cycle, 25°C, and 70% relative humidity. Fifty-five adult male and female *Hogna helluo* were collected from the same habitats as *Pardosa* and bred in captivity in the summer of 1998. The offspring of these

field-collected *Hogna* were used as stimuli for all trials and were maintained in a manner similar to that of *Pardosa*.

Stimulus Preparation. Silk and excreta from *Hogna* of four different sizes were collected on filter paper. One treatment consisted of chemical cues from a large *Hogna* ca. 30 times the body mass of a single *Pardosa* (mean \pm SE = 792.9 ± 15.9 mg). *Hogna* of this size can readily consume up to 10 adult female *Pardosa* in a single feeding bout. A second treatment consisted of silk and excreta from a medium-sized *Hogna* that was approximately equal in size to an adult female *Pardosa* (23.3 ± 1.2 mg). Predation among wolf spiders of equal mass has been shown to be infrequent (Samu et al., 1999). A third treatment used cues from a single small *Hogna* about one half the mass of an adult female *Pardosa* (11.2 ± 1.3 mg) and that can readily be consumed by *Pardosa*. We used a fourth treatment in order to uncouple cue quantity and quality. We collected silk and excreta from eight small *Hogna*, each approximately one fourth the body mass of *Pardosa* (collective mean weight = 54.6 ± 1.8 mg). Each chemical stimulus treatment was paired with a blank sheet of filter paper that had never been exposed to a spider of any size or type (same experimental setup as in Persons et al., 2001). This served as a control to monitor behavioral differences. A fifth treatment consisted of only a blank sheet of filter paper.

All *Hogna* that were used as predator cues were maintained on a diet of appropriately sized crickets (*A. domesticus*) for at least two weeks prior to placing them on filter paper substrates. All stimulus *Hogna* were watered *ad libitum* and fed as many prey as they could consume within a 24-hr period. This was done to minimize any differences in silk production or excreta due to differences in amount of food allocated among groups. *Hogna* were then placed onto sheets of filter paper for 24 hr prior to testing *Pardosa* responses. Each container was previously rinsed with 95% ethanol to remove all extraneous odor cues and allowed to dry. Stimulus spiders for each size treatment had access to a small cap of water in the center of the container. The cap was moved periodically to allow silk or excreta to be deposited beneath it. The lid was closed after *Hogna* were introduced. After the 24-hr period, the filter paper was removed from the container and introduced into a test arena immediately prior to testing. For the treatment consisting of eight *Hogna*, 16 spiders were used for each paper stimulus sheet. Eight spiders were introduced onto a single stimulus sheet of paper and maintained under individual vials to prevent cannibalism or agonistic behavior between individuals. Each set of eight spiders was replaced every 6 hr with another set of eight and allowed to receive water in a separate container. These were then reintroduced onto the substrate under vials again after 6 hr.

Pardosa milvina Testing. Seventy-five adult female *Pardosa* were randomly assigned to one of five treatment pairs ($N = 15/\text{treatment}$). As described above, these treatments were: (1) large *Hogna*/blank, (2) medium *Hogna*/blank, (3) small *Hogna*/blank, (4) eight small *Hogna*/blank, or (5) blank/blank. Test *Pardosa* for

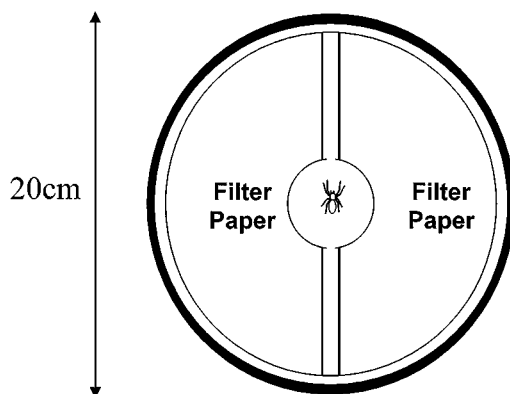


FIG. 1. Experimental apparatus used for testing chemically mediated size discrimination among *Pardosa*. Test spiders are placed in the center of the apparatus and allowed to acclimate for 1 min, after which the spider is allowed to move freely in the container for a period of 1 hr.

each treatment were fed crickets to satiation 24 hr prior to testing and weighed on an analytical balance (27.3 ± 1.0 mg).

We examined the locomotor patterns and behavior of adult female *Pardosa* exposed to each treatment pair and across pairs. Test arenas for *Pardosa* were 20-cm-diam. \times 8-cm-high plastic containers consisting of two half circles of filter paper that collectively covered most of the surface area of the arena except for a 5- to 6-mm band between the two sheets (Figure 1). Additionally, a half circle was cut in the center of each sheet, and this area was used to introduce the spider.

Each spider was introduced into the center of the arena under a clear plastic vial. Each of the 15 spiders per treatment pair was presented a stimulus from a different *Hogna* of the appropriate size class, and no filter paper sheets were used more than once. After a 1-min acclimation period, spiders were allowed to move across the paired treatments for 1 hr each. Spatial positions of filter paper treatments within pairings were randomized among test subjects to eliminate any potential side bias. The test arena was swabbed with 95% ethanol between stimulus presentations to each subject and allowed to dry. Test trials were illuminated equally on all sides with four 15-W fluorescent lights installed in a square configuration above the testing arena. All spiders were tested between 07:00 and 19:00 hr.

Locomotor behavior was measured by monitoring the spiders remotely using an automated digital data collection system (Videomex-V, Columbus Instruments, Columbus, Ohio, USA) integrated into a video camera (JVC high band Saticon GXS 700). All behaviors were recorded automatically. For each test spider,

we recorded the following behaviors separately for each filter paper treatment: (1) time spent moving forward (locomotion), (2) time spent in nonforward movement (any movement of the appendages or turning of the body in place without forward locomotion), (3) time spent immobile (no visible indications of movement), (4) distance traveled (centimeters), (5) residence time (time spent on filter paper), and (6) speed (distance traveled/time spent moving forward). We also recorded the initial choice of sides for each pairing. Changes in spider movement were recorded every second and required a movement of at least one body length in that time period to be measured as forward movement. All locomotor patterns were output onto a computer printer every 5 min, and behaviors for each subject were summed over the 1-hr period.

Statistical Analyses. Because none of the behavior classes showed deviations from a normal distribution (Wilk-Shapiro normality statistic), parametric statistics were used for analyses. We used paired *t* tests to compare behavioral differences between paired filter paper treatments for each class of behavior. We used ANOVA to determine differences for each behavioral category across the three size class treatments and the blank control. A planned series of two-sample *t* tests was used to test for differences for each class of behavior between the eight *Hogna* treatment versus the medium *Hogna* treatment. This was done to determine if *Pardosa* behavior is the result of variation in the quantity or quality of *Hogna* cues.

A second set of analyses was done to compare differences in spider responses across each *Hogna* size treatment. Six one-way ANOVAs were completed with residence time, time in forward locomotion, time in nonforward locomotion, distance moved, time spent immobile, and speed as dependent variables for the blank, large *Hogna*, medium *Hogna*, and small *Hogna* size treatments. Each stimulus treatment paired with a blank was used as the independent variable. Chi-squared goodness of fit tests were used to determine differences in initial choice of sides in each treatment pairing.

RESULTS

In general, there was a decrease in *Pardosa* activity with cues from *Hogna* of increasing size. *Pardosa* showed a significant reduction in activity in the presence of all *Hogna* size treatment groups compared to blank controls except when on substrates from the small *Hogna* treatment (Figure 2). Based on paired *t* tests, mean time spent immobile and mean residence time were different when the cues were from a medium or large *Hogna* (Figure 2A, B). *Pardosa* spent more time in nonforward locomotion in the presence of cues from large *Hogna* than on a blank control sheet of paper (Figure 2A). There was no difference in any class of locomotor behavior among the double blank treatments, indicating no side bias to the testing container (Figure 2D).

TABLE 1. COMPARISON OF MEAN ACTIVITY LEVELS IN SIX CATEGORIES OF *Pardosa* BEHAVIOR FOR EACH *Hogna* SIZE TREATMENT^a

Behavior	Control	<i>Hogna</i>			$F_{3,59}$	<i>P</i>
		Small	Medium	Large		
Residence time (sec)	1608.90 a	2153.30 ab	2431.30 b	2577.7 b	4.06	0.0111
Forward locomotion (sec)	267.46	175.00	242.33	228.87	0.80	0.5024
Nonforward movement (sec)	382.47	394.13	460.87	540.33	0.99	0.4049
Distance moved (cm)	1107.6 a	354.70 b	498.95 b	551.06 ab	4.31	0.0084
Time immobile (sec)	891.33 a	1566.90 ab	1719.60 ab	1828.30 b	3.32	0.0262
Speed (cm/sec)	3.31 a	1.77 b	1.79 b	2.18 b	7.32	0.0003

^aDifferent letters indicate significant differences between *Hogna* size treatment groups based on a Tukey post-hoc comparison of means test. *F* ratios are based on one-way ANOVAs. *N* = 15/treatment.

There was a significant difference in total time spent on each *Hogna* treatment (Table 1). Based on a Tukey *post-hoc* comparison of means, *Pardosa* spent longer periods of time on the medium and large *Hogna* treatments compared to the control. Residence time on the small *Hogna* treatment was intermediate between the control and other *Hogna* size treatments (Table 1). There was no difference in forward locomotion or nonforward locomotion across any size treatment group (Table 1). The total mean distance moved was different, with *Pardosa* traveling shorter distances on the small *Hogna* and medium *Hogna* treatments compared to the control substrate. Distance moved on the large *Hogna* substrate was intermediate between the control and other size treatments (Table 1). Time spent immobile was different on the large *Hogna* treatment compared to the control. Small and medium *Hogna* treatments were intermediate with respect to this behavior (Table 1). Speed of *Pardosa* movement was also measured and compared across treatment groups. Speed was determined by dividing distance moved by time spent in forward locomotion. *Pardosa milvina* moved slower in all *Hogna* size treatments compared to the blank control, but there were no differences in speed across size treatments (Table 1).

To determine if *Pardosa* individuals were responding to quantity of *Hogna* cues, or some qualitative difference in cues based on size, we compared the eight *Hogna* treatment to a blank control and then compared the eight *Hogna* treatment to a treatment of a single medium *Hogna*. *Pardosa milvina* showed a strong and significant reduction in activity in the presence of eight *Hogna* compared to a blank control (Figure 2E). Spiders showed more time immobile and longer residence times on the side with eight *Hogna* compared to the blank control. No other class of behavior differed between pairs. When each behavioral category (nonforward locomotion, forward locomotion, time immobile, residence time, and distance moved) was compared between substrates containing eight small *Hogna* versus a single *Hogna*, there was a significant difference in time spent in nonforward

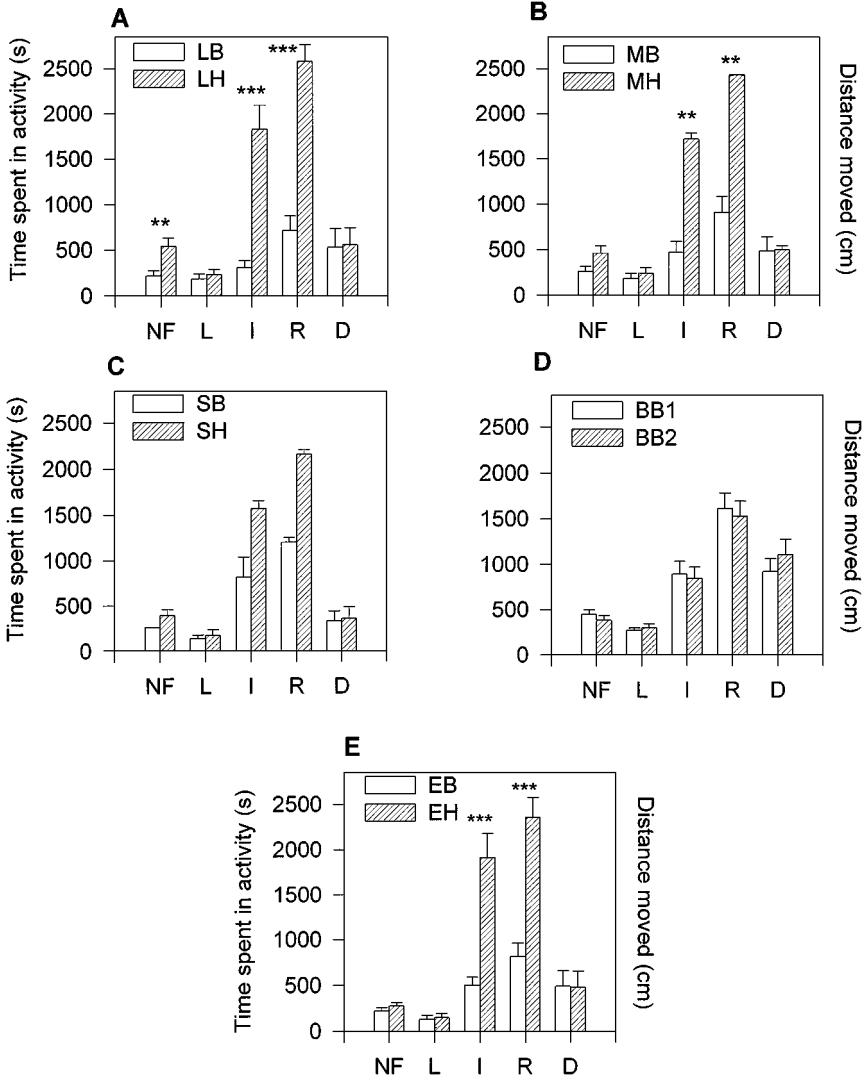


FIG. 2A–E. Comparison of activity level of adult female *Pardosa milvina* exposed to paired treatments of filter paper previously occupied by *Hogna* of different sizes or a blank sheet of paper. Behavioral categories on ordinate are as follows: NF = time spent in nonforward locomotion, L = time spent moving forward (locomote), I = time spent immobile, R = residence time on that substrate, D = distance moved. Distance moved is measured in centimeters and is represented on the same scale as time. All other behaviors are measured in seconds. Results are expressed as means ($N = 15/\text{treatment}$) \pm SE. Significance levels are based on paired t tests for each pair of behaviors denoted as follows: * < 0.05, ** < 0.01, *** < 0.001.

TABLE 2. COMPARISON OF MEAN ACTIVITY LEVELS IN SIX CATEGORIES OF *Pardosa* BEHAVIOR FOR EIGHT *Hogna* AND MEDIUM *Hogna* STIMULUS TREATMENTS^a

Behavior	Eight <i>Hogna</i>	Medium <i>Hogna</i>	T_{28}	P
Residence time (sec)	2353.9	2431.30	0.24	0.809
Forward locomotion (sec)	151.00	242.33	1.23	0.238
Nonforward movement (sec)	275.27	460.87	2.10	0.045
Distance moved (cm)	478.37	498.95	0.09	0.929
Time immobile (sec)	1910.30	1719.60	0.51	0.615
Speed (cm/sec)	2.32	1.793	1.30	0.203

^aResults are based on two-sample t tests. $N = 15$ /treatment.

locomotion (Table 2). Spiders spent more time engaged in nonforward movement in the medium *Hogna* treatment compared to the eight *Hogna* treatment. However, there were no other behavioral differences between the two treatments (Table 2).

Avoidance behavior was found only when *Pardosa* encountered chemical cues from large *Hogna*. When given a choice between a blank sheet of paper and one with cues from an adult female *Hogna*, spiders chose the blank side more often than expected by chance (12 of 15, $\chi^2 = 5.4$, df 14, $P < 0.025$). *Pardosa milvina* showed no initial side preference when given a choice between a blank sheet and *Hogna* cues from medium *Hogna*, small *Hogna*, or eight *Hogna*.

DISCUSSION

In general, *Pardosa* spiders showed reduced activity in the presence of cues from *Hogna* of increasing size. The most commonly modified behavior was time spent immobile. This also explains the counterintuitive response of spiders spending more time on substrates with *Hogna* cues. *Pardosa* tend to become immediately quiescent upon contact with *Hogna* silk and excreta. Spiders also showed a drop in distance moved across *Hogna* size treatments, suggesting it takes much longer for *Pardosa* to leave these substrates than when encountering areas devoid of *Hogna* cues.

*** <0.001. (A) Chemical cues from large adult female *Hogna* (LH) vs. a blank (LB). (B) Chemical cues from a medium-sized *Hogna* (MH) equal in body mass to the *Pardosa* being tested vs. a blank control (MB). (C) chemical cues from a small *Hogna* (SH) half the body mass of the test spider vs. a blank (SB). (D) a double blank control, B1 and B2. (E) chemical cues from eight small *Hogna* (EH) each ca. one fourth the mass of the *Pardosa* being tested vs. a blank control (EB). Locomotor activity and initial side choice was recorded for each spider.

The overall locomotor behaviors for each *Hogna* size treatment appeared to be qualitatively the same. Although *Pardosa* responses to the small *Hogna* treatment were not significant compared to the control (Figure 2), this appears to be due to a difference in the magnitude of the response. This suggests that variation in the quantity of cue is responsible for variation in *Pardosa* reduction in movement. Moreover, compared to a control sheet, *Pardosa* had a reduction in speed as well as distance moved on the small *Hogna* treatment (Table 1). *Pardosa* exhibited a strong reduction in movement to eight *Hogna*, which appears to be a response equivalent to a medium or large *Hogna*. Since none of the eight small *Hogna* would present a predation threat, these data suggest that it is the quantity of cues that serves as the proximate source of information governing the degree of antipredatory behavior.

Other studies have shown that long periods of immobility greatly increase survival probabilities of *Pardosa* when in the presence of a large *Hogna* (Persons et al., 2001). Reduced locomotion is likely to be adaptive since wolf spider visual systems are strongly biased toward movement rather than shape cues (Rovner, 1996). Wolf spiders are much more likely to lunge at prey that move for longer periods of time (Persons and Uetz, 1997), and reduction in locomotion reduces vibrations generated through the substratum that could also be used by a predatory wolf spider to locate prey (Lizotte and Rovner, 1988).

Pardosa milvina exhibits graded antipredator responses with variation in perceived risk of predation; however, chemical cues alone provide insufficient information for an individual to discriminate between a single large *Hogna* or many smaller individuals. We cannot rule out the possibility that a high density of silk and excreta from large numbers of *Hogna* spiderlings may be an indicator of an adult female *Hogna* nearby. We have found single female *Hogna* capable of producing over 200 offspring (personal observation). The young are carried on the mother's back for a short period of time and then disperse. We believe spiderlings of the same species would rarely occur at densities high enough to produce the amount of kairomone used in this study except immediately after dispersal. It is possible that *Pardosa* could interpret such information as the presence of a large adult female *Hogna* in the area. Without visual, vibratory, or tactile cues to confirm the size of the *Hogna*, *Pardosa* appears to treat any quantity of silk and excreta equal to or greater than that which they produce as a potential predation threat. Nonetheless, *Pardosa* responses to substrates would result in a close match between appropriate antipredator response and the actual risk of predation in most cases. *Pardosa* showed an avoidance response to adult female *Hogna*, the only size class in these treatments that would pose a large potential predation risk. The fact that potential prey apparently can induce significant, albeit lower levels of antipredator behavior, suggests that *Pardosa* weighs the fitness costs of predation more heavily than the loss of a meal. Previous studies have demonstrated that *Pardosa* is unresponsive to silk and excreta from equal-sized conspecifics (Persons et al., 2001), but in this study, *Pardosa* showed

antipredator responses to *Hogna* of equal size. These results suggest that *Pardosa* is capable of discriminating between conspecific and heterospecific silk and excreta.

In general, the results show limited support for two of our three original predictions. Adult female *Pardosa* showed increasing levels of antipredator behavior in the presence of chemical cues from *Hogna* of increasing size. However, *Pardosa* showed significant levels of antipredator behavior in the presence of a *Hogna* equal in size to itself and showed some antipredator behavior, although this was not always statistically significant, in the presence of small *Hogna*. Adult female *Pardosa* appeared to increase antipredator behavior in the presence of increased quantities of chemical cues from *Hogna*, even when those cues were produced from *Hogna* that could be eaten by *Pardosa*. Finally, when given a choice, *Pardosa* tended to avoid substrates previously occupied by a *Hogna* larger than itself, but showed no substrate avoidance if the paper had supported a spider or spiders of equal or smaller size to itself. This indicates that whatever the mechanism, *Pardosa* generally demonstrates antipredator responses appropriate to the degree of predation risk.

Acknowledgments—We thank Doug Meikle for the use of video equipment and lab space for this study. We also thank Leah Winkler, Marie Wills, Mike Brueseke, Tara LaFever, Stephanie Sieg, and Dean Ferrera for their help in collecting and maintaining spiders in the lab. This research was funded by NSF grant DEB 9527710 (for A. Rypstra and S. Marshall), the Department of Zoology, Miami University Research Challenge Grant, and the Hamilton Campus of Miami University.

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