ANIMAL BEHAVIOUR, 2001, **61**, 43–51
doi:10.1006/anbe.2000.1594, available online at http://www.idealibrary.com on IDEAL®

Wolf spider predator avoidance tactics and survival in the presence of diet-associated predator cues (Araneae: Lycosidae)

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(Received 9 July 1999; initial acceptance 4 October 1999;
final acceptance 6 June 2000; MS. number: A8547R)

Some prey can distinguish between chemical cues from predators fed different diets. Here we document the first evidence of diet-based chemical discrimination of predators in a terrestrial arthropod and measure the survival value of behavioural responses to predator chemical cues. We tested activity level and avoidance behaviour of the wolf spider, *Pardosa milvina*, to faeces and silk associated with the predatory wolf spider, *Hogna helluo*, fed either *P. milvina* or crickets (*Acheta domesticus*). We then measured survival of *Pardosa* in the presence of *Hogna* when placed on blank paper or paper previously occupied by *Hogna* fed either crickets or *Pardosa*. Filter paper previously occupied by *Hogna* from each diet treatment or a blank control were simultaneously presented to adult female *Pardosa* among four treatment pairs (N=15/treatment): (1) blank paper/blank paper, (2) *Hogna* fed crickets/blank, (3) *Hogna* fed *Pardosa*/blank and (4) *Hogna* fed *Pardosa*/*Hogna* fed crickets. Cues from *Hogna* fed either crickets or *Pardosa* elicited significantly less activity relative to blank controls. Cues from *Hogna* fed *Pardosa* elicited a significantly greater reduction in activity than *Hogna* fed crickets. When given a choice, *Pardosa* initially chose the blank substrate significantly more often than either substrate with *Hogna* cues. Spiders survived longer in the presence of cues from either *Hogna* diet treatment relative to blank paper, but there was no significant effect of predator diet on survival. Results suggest diet-based predator cues elicit different levels of activity in *Pardosa* that reduce predation in the presence of *Hogna*.

Animals that range widely through the environment generally have little information about the presence of potential predators in a given area. Early detection and recognition of a predation threat should increase the ability to avoid predation effectively. Therefore, highly mobile animals may especially benefit from the use of indirect cues such as faeces or other metabolic by-products to detect predators than if relying on visual, substratum-borne vibrations, or tactile cues alone. Many animals display a number of defensive behaviours when encountering chemical cues associated with predators (reviewed in Kats & Dill 1998). However, these behaviours are generally costly in that they can interfere with both foraging and reproductive behaviour (reviewed in Lima & Dill 1990; but see Sih 1980; Gilliam & Fraser 1987; Travers & Sih 1991; Forsgren 1992; Berglund 1993; Hedrick & Dill 1993; Godin 1995). Therefore, if an animal can assess predation risk accurately, it may mitigate these costs by exhibiting antipredator responses proportional to the perceived risk (Lima & Dill 1990).

Studies in aquatic systems have revealed numerous species that are not only capable of detecting predators through chemical cues, but are also capable of discriminating between predators that have or have not fed on conspecifics (reviewed in Howe & Harris 1978; Crowl & Covich 1990; Keefe 1992; Wilson & Lefcort 1993; Chivers et al. 1996; Mathis & Hoback 1997; Chivers & Smith 1998). Far fewer studies on diet-associated predator discrimination have been conducted with terrestrial animals (Murray & Jenkins 1999) and, to our knowledge, none with terrestrial arthropods. Often implicit in studies of diet-based predator discrimination is the assumption that predators that have fed on a particular prey type should present a greater predation risk than predators that have fed on other prey. This assumption is presumably based on the idea that increased experience with particular prey types improves search images for that prey (Tinbergen 1960), reduces feeding neophobia (Dutoit et al. 1991; Greenberg 1992), increases handling efficiency, or

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otherwise increases the predator's preference for that prey. However, of the studies that examine predator dietary cues, few test whether or not variation in prey behaviour in the presence of predators fed different diets, results in differential predation of those prey (Chivers et al. 1996). Furthermore, it is often unclear whether predators fed different diets actually constitute different levels of predation risk for prey through diet preferences, attack efficiency, or other measures of risk.

We chose to test variation in wolf spider responses to predator dietary cues for a number of reasons. First, such studies appear to be lacking for terrestrial arthropods (Kats & Dill 1998). Second, in addition to faecal cues, wolf spiders frequently leave a dragline of silk as they move through the environment that could be used as a source of information for both predators and prey. Third, wolf spiders commonly feed on each other, so the chemosensory structures necessary to perceive faeces or silk cues in the prey are also likely to be similarly developed in the predator. Finally, at least one species of wolf spider, *Hogna helluo*, changes its prey preference based on its most recently consumed prey (Persons & Rypstra 2000).

Hogna helluo and *Pardosa milvina* are syntopic species of wolf spider and are among the most abundant ground-dwelling spiders within agricultural fields of the eastern and central United States (Dondale & Redner 1990; Young & Edwards 1990; Marshall & Rypstra 1999). *Hogna* occurs in densities of up to one individual/m^2 and *Pardosa* is found in densities of about five individuals/m^2; therefore, these two species are likely to encounter each other frequently (Marshall & Rypstra 1999). *Hogna* is large (adult females ca. 300–800 mg) and may reach 30 times the mass of an adult female *Pardosa*. *Hogna* has been observed feeding on *Pardosa* under natural field condition and, in the laboratory, can consume 10 or more in a single feeding bout (personal observations). Both species are cursorial and do not build webs, but each has somewhat different foraging strategies. *Hogna* is principally a sit-and-wait predator with adult and subadults often producing large amounts of silk. *Hogna* is also a facultative burrower and may produce high concentrations of silk and faeces around the burrow entrance (Walker et al. 1999a). *Pardosa* do not burrow but rather range widely across the landscape and have an active foraging strategy (Walker et al. 1999b). Since *Pardosa* are likely to frequently encounter silk and other predator cues associated with *Hogna* burrows, we hypothesized that *Pardosa* may be able to detect these cues and modify their behaviour in response to a perceived predation threat.

Previous studies have found that even after 9 days without food, *Hogna* is preferentially attracted to chemical cues associated with its most recent prey (Persons & Rypstra 2000). *Hogna* fed *Pardosa* will choose foraging sites associated with chemical cues from *Pardosa*. When fed crickets (*Acheta domesticus*), *Hogna* prefer areas associated with chemical cues from crickets (Persons & Rypstra 2000). Therefore, *Hogna* fed different diets of crickets or *Pardosa* should present different levels of predation risk to *Pardosa*. Based on these studies, we hypothesized that it would be beneficial for *Pardosa* to discriminate between *Hogna* that has or has not preyed on *Pardosa*.

The aim of this study was to examine how chemical cues mediate interactions of *Pardosa* and *Hogna*. It is well known that wolf spider sensory systems are particularly sensitive to movement (Rovner 1996). Wolf spiders are much more likely to attack prey that are moving (Persons & Uetz 1997) and will spend significantly longer periods in foraging patches with moving prey relative to patches with nonmoving prey (Persons & Uetz 1998). Therefore, we predicted that, upon encountering chemical cues from *Hogna*, *Pardosa* would reduce its activity level. If *Pardosa* can recognize the recent feeding history of *Hogna* from these cues, then *Pardosa* should further reduce their activity level in the presence of cues from *Hogna* that have been maintained on a diet of *Pardosa* relative to *Hogna* maintained on a diet of other prey. If reduced activity is to be effective, it must reduce the probability of predation. Thus, we predicted that the same diet-associated cues from *Hogna* that alter the activity level of *Pardosa* should increase *Pardosa* survival in the presence of a hungry *Hogna*.

EXPERIMENT 1: *PARDOSA* RESPONSES TO CUES FROM *HOGNA* ON DIFFERENT DIETS

Methods

Adult female *Pardosa* and adult female *Hogna* were collected from within and beside the margins of soybean fields (Oxford, Ohio, Butler County, Ecology Research Center, Miami University) in June of 1998. Sixty *Pardosa* were used as test subjects to measure behavioural responses on sets of filter paper containing either predator chemical cues or blank controls. Test spiders used for assays of spider activity levels were maintained on a diet of five *Drosophila melanogaster* once a week and were fully sated 24 h prior to testing to minimize hunger effects between spiders (although it has been shown that hunger level has no measurable effect on *Pardosa* locomotor behaviour; Walker et al. 1999b). All test spiders were maintained in plastic translucent containers (8 cm diameter, 5 cm high) and kept in environmental chambers on a 12:12 h light:dark cycle (25°C, 70% RH).

We examined activity levels of field-collected adult female *Pardosa* given a choice between two equal-sized, half-circle sheets of filter paper placed inside a circular test arena (20 cm diameter, 8 cm high; Fig. 1). Each sheet was separated by a 1-cm gap. Combined, the two sheets of filter paper covered the bottom of a plastic container except a small circle in the centre where the test spider was introduced under a clear plastic vial. Within each two-choice arena, we recorded spider behaviour and time spent on each sheet of paper. The filter paper used in the two-choice arenas contained chemical cues deposited from two different types of stimuli or controls: (1) blank sheet of paper (control), (2) *Hogna* fed crickets (low-risk predator) and (3) *Hogna* fed *Pardosa* (high-risk predator).

We randomly assigned 15 *Pardosa* to each of four treatment pairs. Treatments consisted of the following paired chemical stimuli on filter paper: (1) a clean, blank

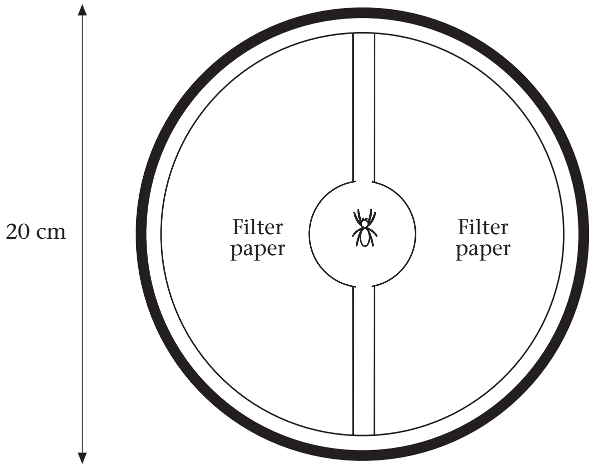

Figure 1. Experimental apparatus used for testing chemically mediated predator-diet discrimination among *Pardosa milvina*. Test spiders were placed in the centre of the apparatus and allowed to acclimate for 1 min, after which the spider was allowed to move freely in the container for 1 h.

sheet of filter paper (Whatman number 1) paired with another blank sheet, (2) chemical cues from a *Hogna* fed crickets paired with a blank, (3) cues from a *Hogna* fed *Pardosa* paired with a blank and (4) cues from *Hogna* fed *Pardosa* paired with *Hogna* fed cricket cues. We provided 30 of the field-collected adult female *Hogna* water ad libitum. We randomly assigned 15 *Hogna* to a diet of two medium-sized crickets twice a week (*Acheta domesticus*) (ca. 1 cm in length). We fed the other 15 *Hogna* four adult *Pardosa* twice a week for at least 2 weeks prior to the experiment. Two days prior to the experiment, we fed both *Hogna* diet-treatment groups as many assigned prey as they would eat within a 24-h period. This was done to minimize any differences in silk production or faeces due to differences in the amount of food allocated between groups. We then placed each *Hogna* in a separate container lined with a single sheet of filter paper for 24 h prior to testing *Pardosa* responses. We previously rinsed each container with 95% ethanol to remove any residual chemical cues and allowed them to dry. Immediately after removal of the *Hogna*, we transferred the paper to the separate test arena and introduced a test *Pardosa*.

We initially introduced spiders into the test arena under an inverted, clear 3-cm diameter vial for 1 min, after which we removed the vial and allowed the spider to move freely for 1 h. We presented each spider with either a blank sheet of paper, cues from *Hogna* fed *Pardosa*, or cues from *Hogna* fed crickets. Each sheet of filter paper contained cues from a different individual and no sheet was used more than once. All spiders were tested between 0700 and 1900 hours. For each spider, we recorded the following behaviours separately for each filter paper treatment: (1) time spent moving forward (walking), (2) time spent in nonforward movement (any movement of the appendages or turning of the body in place without walking), (3) time spent immobile (no visible indications of movement), (4) distance travelled (cm), (5) residence time (time spent on filter paper) and (6) speed of movement, derived by dividing distance travelled by time spent moving forward. We also recorded the initial choice of sides for each pairing. We randomized spatial positions of filter paper treatments within pairings 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.

We measured spider movements by monitoring the spiders remotely using an automated digital data collection system (Videomex-V, Columbus Instruments, Columbus, Ohio, U.S.A) integrated into a video camera (JVC high band Saticon GXS 700). All locomotor behaviour was recorded automatically. Changes in spider movement were recorded every second and required a movement of at least one body length in that time period to be scored as walking. All spider movements were outputted through a computer printer every 5 min and behaviours for each subject were summed over a 1-h period.

Because none of the behaviour classes showed significant deviations from a normal distribution (Wilk–Shapiro normality statistic, Statistix®: Analytical Software 1996), we used parametric statistics for all analyses. We used paired *t* tests to compare behavioural differences between paired filter paper treatments. We used chi-squared goodness-of-fit tests to determine significant differences in initial choice of sides in each treatment pairing.

Results

Pardosa activity levels differed significantly between *Hogna* diet treatments. When *Pardosa* were allowed to move between substrates previously occupied by *Hogna* fed crickets or *Hogna* fed *Pardosa*, *Pardosa* showed significantly longer periods of immobility, more nonforward movement, and longer residence time in the presence of cues from *Hogna* fed *Pardosa* than *Hogna* fed crickets (Fig. 2a). Spiders showed no difference in the time spent walking or distance travelled between the two *Hogna* diet treatments. There was also no significant difference in mean *Pardosa* speed across the two *Hogna* diet treatments (Fig. 3).

To test for possible avoidance of substrates with *Hogna* chemical cues, we performed two additional pairings to examine *Pardosa* behaviour when presented either *Hogna* fed crickets or *Hogna* fed *Pardosa* and a blank (Fig. 2b and c, respectively). These pairings also allowed us to examine any changes in behaviour when the spider was given a clear choice between predator cues and a blank. When spiders were given a choice between a blank control and a *Hogna* fed either prey type (Fig. 2b, c), spiders showed a significant reduction in activity on the *Hogna*-treated side of the arena. For both *Hogna* fed crickets and *Hogna* fed *Pardosa* treatments, large differences were found in activity levels between the *Hogna* treatment and the blank for each pair, but the magnitude of activity reduction was greater when spiders were presented substrates from *Hogna* that had fed on *Pardosa* (Fig. 2c). *Pardosa* showed significantly longer periods of immobility, longer residence time and increased nonforward movement in the presence of both *Hogna* diet treatment compared with blank controls (Fig. 2b, c). These results were consistent

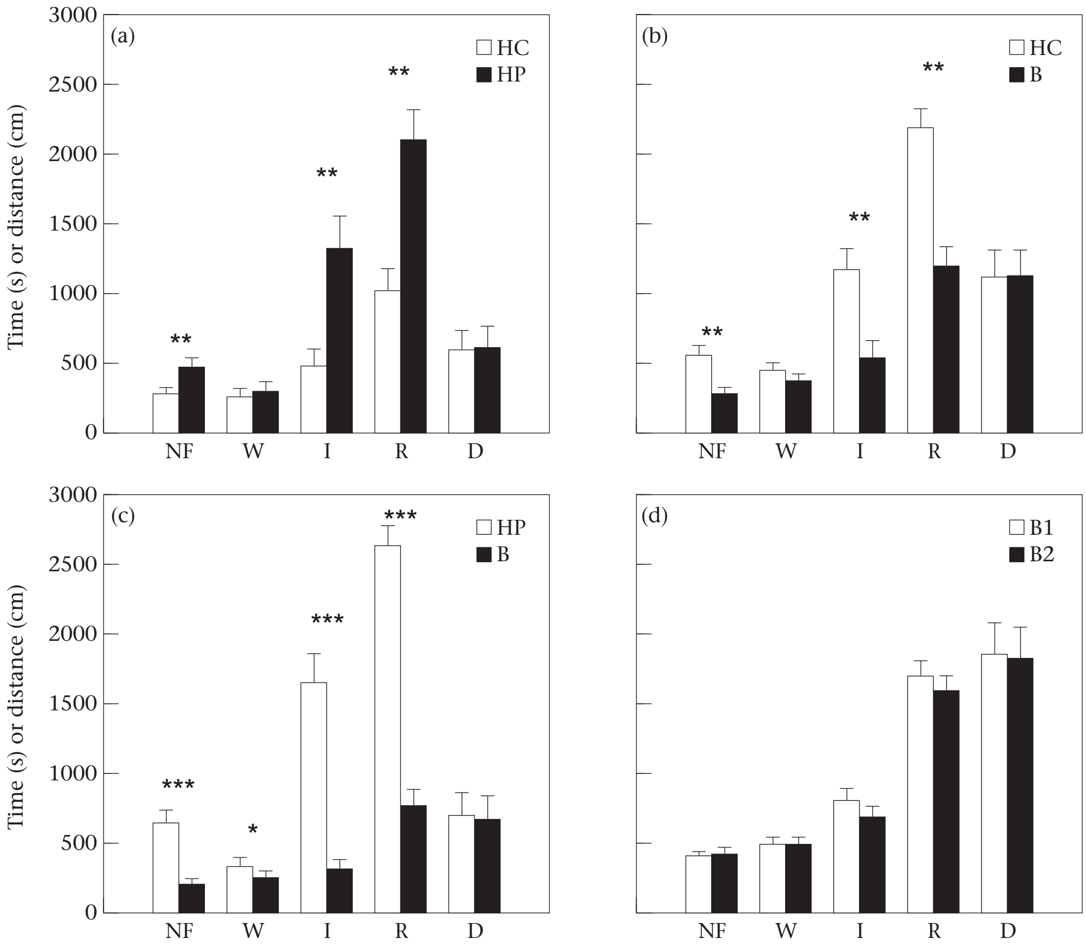

Figure 2. Mean+SE activity levels of adult female *Pardosa milvina* exposed to paired treatments of filter paper previously occupied by *Hogna helluo* maintained on different diets or blank controls (N=15/treatment). HP: Cues from *Hogna* fed *Pardosa*; HC: cues from *Hogna* fed crickets; B: blank control. (a) Cues from *Hogna* fed *Pardosa* versus *Hogna* fed crickets. (b) Cues from *Hogna* fed crickets versus a blank control. (c) Cues from *Hogna* fed *Pardosa* versus a blank control. (d) A double blank control. NF: Nonforward movement; W: walking; I: immobile; R: residence time; D: distance moved. Distance moved is measured in centimeters and is represented on the same scale as time. All other behaviours are measured in seconds. Significance levels are based on paired t tests for each pair of behaviours: *$P<0.05$; **$P<0.01$; ***$P<0.001$.

with the *Hogna* fed *Pardosa*/*Hogna* fed cricket pairing, which indicated an ability to discriminate between *Hogna* based on diet by reducing activity with increased predation risk. *Pardosa* also travelled at significantly lower speeds in both *Hogna* diet treatments relative to blank controls (Fig. 3).

To determine baseline levels of activity in the absence of any stimuli, we tested a double blank pairing. There were no significant differences in any activity measurement in the double blank pairing, indicating a lack of side bias in the apparatus (Fig. 2d). These results also indicate that spiders travelled longer distances, spent less time immobile and had shorter residence time on blank substrates than on substrates previously occupied by *Hogna* (Fig. 2d). Some individuals were observed to be in almost constant motion for the duration of the 1-h trial, which demonstrates that low activity levels by *Pardosa* in the presence of *Hogna* cues is not commonly displayed in the absence of predator chemical stimuli. There was also no significant difference in *Pardosa*'s speed of movement in the double blank pairing (Fig. 3).

Pardosa presented a choice between cues from *Hogna* fed *Pardosa* or a blank initially walked towards the blank side significantly more often (χ^2_1=8.07, P<0.005) and also chose to walk to the blank side significantly more often when paired with cues from *Hogna* fed crickets (χ^2_1=5.4, P<0.025). When presented pairings of cues from either a *Hogna* fed *Pardosa* or *Hogna* fed crickets, *Pardosa* showed no initial side preference (χ^2_1=0.6, NS). Nor did *Pardosa* exhibit a significant initial side preference when given a choice between two blanks (χ^2_1=0.06, NS).

EXPERIMENT 2: *PARDOSA* RESPONSES TO CONSPECIFIC CUES

Methods

It is possible that *Pardosa* reduce activity in the presence of any biogenically produced chemical cue, not necessarily only cues produced by predators. To test for this possibility, we measured differences in *Pardosa* locomotor

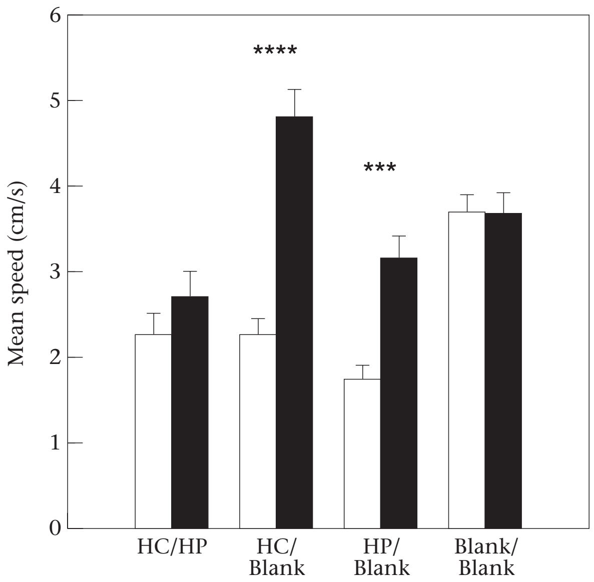

Figure 3. Mean+SE speed of movement of *Pardosa milvina* exposed to paired treatments of filter paper previously occupied by *Hogna helluo* fed different diets. Category designations are as in Fig. 2. Significance levels are based on paired *t* tests for each pair of behaviours: *P<0.05; **P<0.01; ***P< 0.001; ****P<0.0001.

behaviour in the presence of a blank sheet of paper paired with paper previously occupied for 24 h by a conspecific adult female. All protocols, equipment and behavioural measurements were identical to those in experiment 1 except that chemical cues from a single adult female *Pardosa* were used as a stimulus rather than cues from an adult female *Hogna*. We maintained 15 *Pardosa* on an ad libitum diet of *A. domesticus* 24 h prior to placing them on the filter paper substrate. Each of 15 test *Pardosa* were similarly satiated on *D. melanogaster* 24 h prior to being placed in the test arena. Following introduction into the test arena, we allowed each test spider to move freely on each of the two sheets of paper for 1 h and we recorded locomotor behaviour as in experiment 1. No spider was used as both a test subject and a source of chemical cues and each spider was used only once.

Results

Pardosa showed no significant response to paper containing conspecific cues relative to the control (Fig. 4). Based on six separate paired *t* tests (α=0.05), there was no significant difference in time spent walking, time spent immobile, residence time, time spent in nonforward locomotion, or distance travelled among each substrate type (N=15). Spiders showed no significant difference in average speed of movement. *Pardosa* showed a mean speed of 4.13 cm/s on blank substrates compared to 3.82 cm/s on substrates previously occupied by *Pardosa* (paired *t* test: $t_{1,\,14}$=0.65, P=0.52). There was also no significant initial side preference (χ^2_1=1.20, P=0.2733).

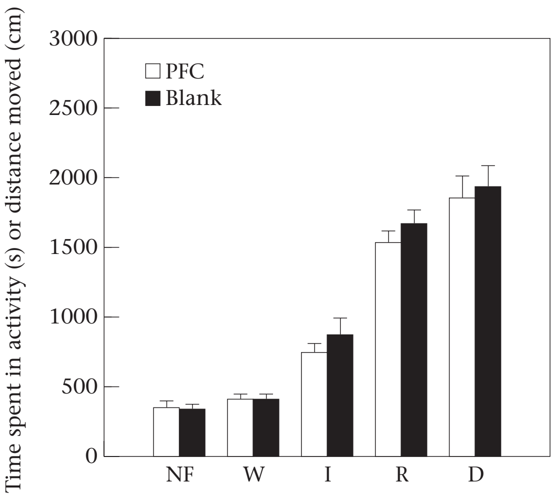

Figure 4. Mean+SE activity levels of adult female *Pardosa milvina* exposed to paired treatments of filter paper previously occupied by *Pardosa* maintained on crickets or blank controls (N=15/treatment). PFC: Cues from *Pardosa* fed crickets; B: blank control. All other category designations as in Fig. 2. Paired *t* tests for each pair of behaviours: NS.

EXPERIMENT 3: *PARDOSA* SURVIVAL ON PAPER WITH DIFFERENT *HOGNA* DIET TREATMENTS

Methods

We tested the survivorship of *Pardosa* exposed to *Hogna* in the presence or absence of chemical cues from *Hogna* fed either *Pardosa* or crickets (*A. domesticus*). *Pardosa* were maintained in 100-ml opaque, colourless containers (8 cm diameter, 5 cm high) and fed five fruit flies (*D. melanogaster*) once weekly for 2 weeks prior to testing.

Hogna were maintained in 550-ml opaque containers (7.5 cm diameter, 11 cm high). We fed one set of *Hogna* (N=36) a diet of three mealworm beetle larvae (*Tenebrio molitor*) weekly for at least 1 month prior to their use as experimental predators for this experiment. We fed neither crickets nor *Pardosa* to ensure that there would not be any confounding effects of prey preference, capture experience, or additive chemical cues. We fed two other sets of *Hogna* either crickets (N=12), or adult female *Pardosa* (N=12) ad libitum once weekly for a month prior to testing, and used them as sources for chemical cues. *Hogna* maintained on mealworms were fed to satiation, then fasted for 2 weeks prior to testing to standardize hunger levels. *Hogna* fed *Pardosa* or crickets were fed to satiation 24 h prior to being introduced on filter paper substrates. We exposed *Pardosa* to *Hogna* in circular plastic arenas (20 cm diameter, 8 cm high) with a single sheet of filter paper completely covering the bottom (same type of container used for experiment 1 and 2).

We used three different treatments (N=12/treatment): (1) a blank paper control, (2) paper previously occupied by *Hogna* fed crickets for 24 h prior to testing, and (3) paper previously occupied by *Hogna* fed *Pardosa* for 24 h prior to testing. We removed stimulus spiders fed either *Pardosa* or crickets and then immediately introduced single adult female *Pardosa* into each of 12 replicates

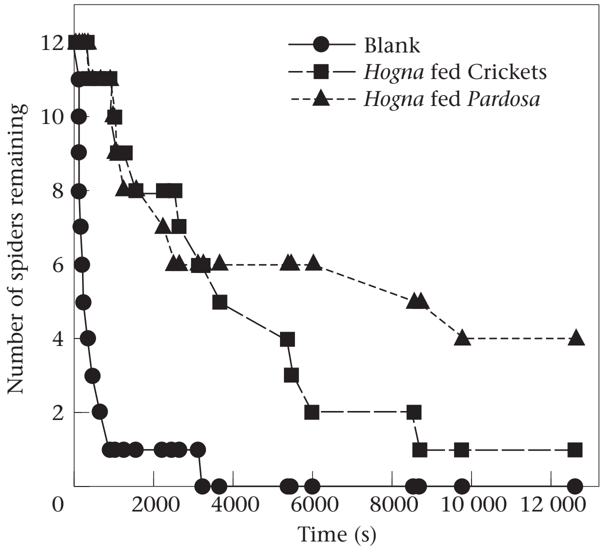

Figure 5. Survival of *Pardosa milvina* over time in containers with adult *Hogna helluo* paired with chemical cues from *Hogna* fed crickets, *Hogna* fed *Pardosa*, or containers devoid of cues (blank).

for the three treatment groups. We allowed *Pardosa* to acclimate for 30 min and then we introduced a *Hogna* fed mealworms into each container by placing it under an inverted plastic vial for 3 min and then removing the vial. We recorded attack latency (s), or the time it took the *Hogna* to actually prey on the *Pardosa*. The experiment was terminated after 3.5 h of continuous observation. The observations in this data set consisted of time until *Pardosa* death during the 3.5-h period. We used a nonparametric failure-time analysis using the Kaplan–Meier product limit estimator to compare differences in survival distribution and test for a significant treatment effect (Statview, SAS Institute 1998; Cox & Oakes 1984). We used a nonparametric statistic because the survival of *Pardosa* over the 3.5-h period tended toward a negative exponential distribution. We then made pairwise comparisons of the survival distributions using the log-rank (Mantel–Cox) test (Statview, SAS Institute 1998).

Results

Pardosa survived longer in the presence of *Hogna* chemical cues from either diet treatment compared with control containers. Based on a Kaplan–Meier failure-time analysis, there was a large overall treatment effect on *Pardosa* survival (Mantel–Cox test: $\chi^2_2=29.052$, $P<0.0001$). There were significant differences in median survival time between the blank and *Hogna* fed cricket treatment (Mantel–Cox test: $\chi^2_1=16.447$, $P<0.0001$), as well as the blank and *Hogna* fed *Pardosa* treatment (Mantel–Cox test: $\chi^2_1=16.447$, $P<0.0001$) (Fig. 5). More *Pardosa* survived when on substrates from *Hogna* fed *Pardosa* than either *Hogna* fed crickets or blank controls (Fig. 5). However, there was no significant difference in median survival between the two diet treatments (Mantel–Cox test: $\chi^2_1=1.295$, $P=0.26$; Fig. 5).

DISCUSSION

These results demonstrate that *P. milvina* wolf spiders detect and respond to chemical cues deposited by a predator, *H. helluo*. *Pardosa milvina* not only reduce activity levels in the presence of cues from *Hogna*, but also appear to react more strongly when a *Hogna* has been feeding on other *Pardosa* compared with another prey type. In addition, the presence of these chemical cues enhances *Pardosa* survival when spiders are paired with live *Hogna*. However, even though *Pardosa* responded differently to cues from *Hogna* fed different diets, such differences did not translate into differential survival in the presence of a live *Hogna*.

Our data are consistent with the hypothesis that reduced activity and avoidance behaviour in the presence of chemical cues from *Hogna* function as a predator avoidance tactic. *Pardosa* may modify activity levels according to the perceived predation risk. However, animals may reduce activity for reasons other than predator avoidance. Our experimental design did not explicitly test for alternative explanations of reduced *Pardosa* activity. *Pardosa* may show similar reductions in activity whenever it encounters chemical cues from prey or other stimuli. As such, this behaviour could be interpreted as investigative or exploratory rather than antipredatory. However, we believe this behaviour functions as a predator avoidance tactic in *Pardosa* for a number of reasons. Adult female *Pardosa* showed no reduction in activity in the presence of conspecific female silk and faeces relative to control substrates (Fig. 4). Also, *Pardosa* showed significant avoidance of paper containing silk and faeces from *Hogna*, but did not show similar avoidance of silk and faeces from conspecifics (Fig. 4). Collectively, these data suggest that reduced activity and avoidance is a response specific to silk and faeces of *Hogna* rather than silk and faeces of any spider.

Our hypothesis that reduced activity in the presence of *Hogna* cues increases survival is supported by the large difference in survival between *Pardosa* placed in containers with or without *Hogna* chemical cues. Reduced *Pardosa* activity did not appear to be strongly influenced by other sensory cues from *Hogna*. Although it is likely that *Pardosa* could detect *Hogna* through a combination of visual cues, substratum-borne vibratory cues, tactile cues, and possibly airborne cues, these were insufficient to induce any obvious reduction in activity or obliterate survival differences between treatments. This suggests that the proximate sensory cue used to induce reduced activity is primarily the chemical cues associated with *Hogna* rather than other sensory information. The fact that *Pardosa* initially avoided substrates with *Hogna* cues prior to contact with the substrate, suggests that an airborne chemical cue may be involved in predator detection. Male *Pardosa* are known to respond to an airborne pheromone from female conspecifics. Therefore, we believe that *Pardosa* may be likely to possess the chemosensory structures necessary to detect an airborne kairomone as well (Searcy et al. 1999). Although visual detection of *Hogna* faeces and silk cannot be ruled out as an avoidance cue, this seems unlikely. Silk and faeces are nonmoving and light coloured on a white background and would therefore be difficult for a wolf spider to detect visually.

During experiment 3, *Pardosa* appeared to show a large reduction in activity when placed in containers with *Hogna* chemical cues compared with containers lacking such cues. We did not explicitly measure activity levels during this experiment, however, and could not statistically confirm reduction in activity during the experiment. An alternative explanation for variation in *Pardosa* survival across substrate treatments is that *Hogna* modified its behaviour in the presence of chemical cues from conspecifics and this behaviour, in turn, reduced its foraging success. Our experimental design did not allow discrimination between these two equally plausible explanations.

Given that there is extensive evidence of predator chemical cues being important in eliciting antipredator behaviour in other taxa, it is suprising that there are few studies of chemically mediated predator–prey interactions in spiders (Persons & Uetz 1996a; Punzo 1997; Punzo & Kukoyi 1997; Persons & Rypstra 2000). Punzo (1997) found that the wolf spider *Schizocosa avida* is able to detect chemical cues from the predatory scorpion *Centruroides vittatus*. Furthermore, *S. avida* that have had previous experience with *C. vittatus* spend less time on substrates previously occupied by *C. vittatus* than do naīve *S. avida*. This suggests that spider predator avoidance tactics may be learned. Since we used field-collected adult female spiders for this study, we do not know whether *Pardosa* responses were learned or innate.

Pardosa behavioural responses suggest that the diet of *Hogna* chemically labels the predator and that *Pardosa* perceives *Hogna* that have been feeding on *Pardosa* as more dangerous. Diet-based chemically labelled predators are known to occur among ostariophysan fish (Mathis et al. 1995; Chivers et al. 1996; Chivers & Smith 1998), sea anemones (Howe & Harris 1978) and damselfly larvae (Chivers et al. 1996). In these cases, the mechanism of diet discrimination has usually been demonstrated to be an alarm pheromone (Brown et al. 1995a, b; reviewed in Smith 1992; Chivers & Smith 1998). Alarm pheromones are generally released only by mechanical damage of the prey during a predation event. Based on our experimental design, we were not able to determine whether an alarm pheromone was the proximate cue that elicited reduced activity in *Pardosa*. However, *Pardosa* showed a strong reduction in activity in response to chemical cues from *Hogna* fed crickets, which suggests that the chemical cues of the predator alone are sufficient to reduce activity and that the diet of the predator likely has an additive effect on this behaviour. It is possible that *Pardosa* could perceive prey cues from *Hogna* fed crickets and that conflicting cues from prey (cricket cues present on *Hogna*) and a predator (*Hogna* itself) caused the observed differences in *Pardosa* activity levels. However, since *Pardosa* failed to show any significant behavioural response to the presence of chemical cues from *Pardosa* fed crickets compared to a blank control, this seems unlikely (Fig. 4).

The presence of cues from *Hogna* results in longer residence times on predator-treated filter paper. This is largely attributable to extended periods of immobility and reduced speed rather than localized searching and increased movement typical of prey detection (Bell 1991; M. H. Persons, unpublished data). *Pardosa* remained motionless for long periods in the presence of *Hogna* cues (Fig. 2a, c) and, when they did move, they tended to move much more slowly than when these predator cues were absent (Fig. 3). Significant differences in mean speed between *Hogna* diet treatments and blank controls appear to be driven not only by reduced speed in the presence of *Hogna* cues, but also increased speed on a blank substrate (Fig. 3). These results indicate that once *Pardosa* is no longer in direct contact with predator chemical cues, it increases its speed to move out of a risky area as quickly as possible.

Although immobility by *Pardosa* resulted in longer residence times on the predator substrate, this may still be adaptive if one considers the biases of wolf spider sensory systems in prey detection. Behavioural studies on how sensory system biases alter predator–prey interactions in wolf spiders are few (but see Persons & Uetz 1996a, b, 1998), but several studies indicate that wolf spider visual senses and vibration detection organs are particularly sensitive to movement cues. Rovner (1996) found that when a blind or sighted *Rabidosa rabida* wolf spider moved, it was unable to detect other conspecifics. Rovner also found that even while motionless, blinded and sighted *R. rabida* males could not detect motionless or slowly moving females. He suggested that slow movement or the absence of motion is a highly effective visual and vibratory form of cryptic locomotion. Other studies have shown that the wolf spider *Schizocosa ocreata* becomes more likely to lunge at televised images of prey when the duration of prey movement is increased and that the spider's residence time in a patch containing prey is closely related to the duration of prey movement in that patch (Persons & Uetz 1997, 1998). Wolf spiders may use both visual and vibratory cues to locate prey (Persons & Uetz 1996b; Lizotte & Rovner 1988) and the cessation of movement is effective at impairing prey detection through either of these sensory channels. Jumping spiders also have increased success locating moving rather than stationary prey (Tarsitano & Jackson 1992). Other taxa have been observed exhibiting 'freezing' behaviour as an effective antipredator behaviour (Hatle & Faragher 1998), especially fish (Brown et al. 1995b; Chivers et al. 1996). Wolf spider activity also significantly affects predation risk by vertebrates (Kotiaho et al. 1998).

Under natural conditions, *P. milvina* range widely over the environment, often occurring in highly disturbed habitats with sparse vegetation and bare soil. Within the soybean fields and margins where these spiders were collected, *Hogna* is likely to be the primary predator of *Pardosa* (Marshall & Rypstra 1999). Numerous studies have examined the influence of physical habitat structure and environmental conditions on wolf spider movement patterns and distribution (Uetz 1975, 1976; Greenquist & Rovner 1976; Cady 1984). Our laboratory observations suggest that the presence of prey and predator cues may be sufficient to modify movement patterns in *Pardosa* in the absence of other environmental factors and that direct encounters with predators and prey are not necessary to change space use and locomotor behaviour in *Pardosa*.

We propose that by discriminating between a high-risk predator (i.e. a *Hogna* that has fed on *Pardosa*) and a low-risk predator (*Hogna* that has fed on crickets), spiders may be able to balance predation risk more closely with other important activities by showing a graded predator avoidance response.

Acknowledgments

We thank Doug Taylor and Doug Meikle for the use of video equipment and space for this study, and M. Brueseke, E. Henley and Dean Ferrera for their help in collecting and maintaining spiders. We also thank Grant Brown and Doug Chivers for discussions leading to these experiments, Alan Cady for reviewing the manuscript and Rob Balfour for technical assistance. This research was funded by NSF Grant DEB 9527710 (for A. Rypstra and S. Marshall), the Department of Zoology, Ohio Board of Regents Research Challenge Grant (for S. Walker) and the Hamilton Campus of Miami University.

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