Fitness costs and benefits of antipredator behavior mediated by chemotactile cues in the wolf spider *Pardosa milvina* (Araneae: Lycosidae)

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Animals may exhibit a variety of defensive behaviors in the presence of indirect predator cues. Such behavior offers immediate fitness benefits but may also incur substantial foraging and reproductive costs. We measured shifts in space use (vertical climbing) by the wolf spider *Pardosa milvina* induced by chemotactile cues (silk and excreta) from a co-occurring predatory wolf spider *Hogna helluo.* We then measured foraging and reproductive costs, as well as survival benefits, of this behavior. For 2 weeks, we maintained mated adult female *Pardosa* in plastic containers with one of three treated peat moss substrates: a container previously occupied by a conspecific for 3 days, a container previously occupied by an adult *Hogna* for 3 days, and a container devoid of either cue (control). We measured prey capture efficiency, body condition, egg sac production, egg sac weight, and egg number for individuals in each treatment. We also counted the number of *Pardosa* that survived and exhibited climbing behavior in the presence of a live *Hogna* with and without silk and excreta cues. *Pardosa* climbed container walls significantly more often in the presence of *Hogna* silk and excreta relative to other treatments. *Pardosa* exposed to *Hogna* cues coupled with live *Hogna* survived significantly longer than spiders that had no predator cues available. *Pardosa* placed in containers with *Hogna* cues, but no *Hogna,* lost weight more quickly, ate fewer prey, were in poorer body condition, produced lighter egg sacs, and produced fewer eggs than spiders in control or conspecific treatments. *Key words:* antipredator behavior, chemotactile cues, *Hogna helluo,* Lycosidae, *Pardosa milvina,* reproductive costs, survival benefits, wolf spiders. *[Behav Ecol 13:386–392 (2002)]*

Prey often exhibit behavioral adaptations to avoid predation such as avoidance (Brown et al., 1995; Gore, 1966), reduced activity (Holomuzki and Short, 1990; Malmqvist, 1992), cover seeking (Kats et al., 1988; Wahle, 1992), or increased vigilance (Sweitzer and Berger, 1992). Early predator detection is often critical for effective use of these tactics. Therefore, many prey have evolved the ability to detect a variety of metabolic by-products associated with the presence of predators and exhibit appropriate behavior even in the absence of the predator itself (reviewed in Chivers and Smith, 1998; Kats and Dill, 1998). Preemptive antipredator tactics may incur substantial fitness costs such as reduced foraging success (reviewed in Lima, 1998; Lima and Dill, 1990) or impaired reproduction (reviewed in Magnhagen, 1991; Kats and Dill, 1998; Repka et al., 1994). These costs may, in turn, translate into a number of life-history changes (Crowl and Covich, 1990) such as delayed development, slower growth (Barry, 1994; Spitze, 1992) or postponed reproduction (Koskela and Ylönen, 1995; Ylönen and Ronkainen, 1994).

Despite an extensive body of literature on prey responses to indirect predator cues, few such studies exist among terrestrial arthropods (Kats and Dill, 1998; Persons et al., 2001; Venzon et al., 2000), and even fewer studies document the costs incurred by arthropods exhibiting chemical or tactile-mediated defensive behavior (Grostal and Dicke, 1999; Hoffmeister and Roitberg, 1997).

Wolf spiders provide an interesting taxon to examine indirectly mediated predator–prey interactions because, in addition to excreta, they also leave a silk dragline behind them while moving through the environment. Because wolf spiders are common prey as well as predators of other species of wolf spider (Persons and Rypstra, 2000), they may be especially likely and able to detect and respond to spider silk and excreta cues. The wolf spider species *Hogna helluo* (Walckenaer) (Araneae: Lycosidae) and *Pardosa milvina* (Hentz) (Araneae: Lycosidae) are syntopic intraguild predators. Both species live in early successional habitats and are often the two most abundant cursorial spiders in agricultural systems of the eastern and central United States (Dondale and Redner, 1990; Marshall and Rypstra, 1999; Young and Edwards, 1990). Neither species constructs a web, and both are typically found on the soil surface or residing on low-lying vegetation, where they feed on a wide variety of ground-dwelling arthropods including cursorial spiders, collembola, and crickets (Persons et al., personal observations). *Hogna* is a large wolf spider (adult female ca. 300–800 mg) and has frequently been observed to prey on the much smaller *Pardosa* (ca. 20 mg) (Persons et al., 2001). *Pardosa* exhibits a variety of defensive tactics when exposed to silk and excreta cues produced by *Hogna,* including prolonged periods of immobility, reduced walking speeds, and substrate avoidance (Persons et al., 2001). These behaviors minimize predation in the presence of *Hogna* (Persons et al., 2001). *Pardosa* has also been anecdotally observed to shift space use by climbing vertical surfaces when exposed to *Hogna* silk and excreta. Behavioral responses may be mediated by chemicals found within silk and excreta, localized structural changes to the substratum, or tactile infor-

mation embedded within the predator cues. For this reason, we refer to behaviorally relevant information found in silk and excreta as chemotactile cues. To date, the potential direct and indirect fitness costs of chemotactile-mediated antipredator behavior has not been experimentally demonstrated in any species of spider.

Female *Pardosa,* like all lycosids, attach their egg sacs to their spinnerets. Egg sacs are energetically expensive to produce, constituting more than 30% of the mass of the spider (Edgar, 1971; Marshall and Gittleman, 1994). Therefore, any behavior that reduces foraging success or results in less energy being available for reproduction should result in a reduction in egg number or egg mass, or a delay in the timing of egg sac production.

Here we addressed possible foraging and reproductive costs as well as survival benefits associated with a shift in space use (vertical climbing) by *Pardosa* when exposed to silk and excreta produced by *Hogna.* We tested the five hypotheses: (1) *Pardosa* should shift their locations to vertical surfaces (climbing movement) in the presence of silk and excreta cues from *Hogna* compared to conspecific silk and excreta or substrates lacking either cue; (2) shifts in space use should result in either reduced foraging success and/or increased energy expenditure as measured by spider body condition; (3) *Pardosa* should reduce feeding in the presence of cues from *Hogna* compared to conspecific cues; (4) long-term exposure to predator chemotactile cues should delayed reproduction and reduce reproductive output; and (5) vertical climbing should increase survival in the presence of live *Hogna* compared to spiders that do not exhibit this behavior.

General spider collection and maintenance

For all experiments we collected adult female *Pardosa* with egg sacs from soybean fields at Miami University's Ecology Research Center (Oxford, Butler County, Ohio, USA) in August 1998. Egg sacs were removed from females within 48 h of any experiment unless otherwise indicated. Adult female *Hogna* with spiderlings or egg sacs were collected from the same soybean fields in August 1997, and their offspring were raised in the lab and used as experimental predators or predator stimuli for all experiments. *Pardosa* were maintained in 5.5 cm high × 5.5 cm diam containers with a 2-cm layer of moistened peat moss covering the bottom. Each container was covered with a clear plastic lid. *Hogna* were maintained in 8 cm high × 12 cm diam white plastic cups with clear lids and also had a 2 cm deep layer of moistened peat moss provided as a source of water and burrowing substrate. Both species were maintained on a diet of domestic house crickets (*Acheta domesticus*).

Experiment 1: measuring behavioral changes and fitness consequences of *Pardosa* exposure to *Hogna* cues

Methods
We measured shifts in space use of mated adult female *Pardosa* when exposed to containers with peat moss substrates previously occupied by one of the following: an adult female *Hogna helluo,* a conspecific female *Pardosa,* or a substrate lacking either cue. Over a 2-week period, we quantified the following for each *Pardosa* within each peat moss treatment: changes in body condition (morphometric measure of weight loss scaled to body size), latency to produce an egg sac, number of egg sacs produced, egg sac weight, and egg number per egg sac. Additionally, *Pardosa* were observed either on the side or bottom of the container, and we used this as our behavioral response variable across each peat moss treatment.

Peat moss stimulus preparation. All test *Pardosa* were ran-domly assigned among containers with three treatment groups of moistened peat moss ($n = 25$/treatment): (1) control, containers devoid of any spider cues; (2) conspecific cues, containers previously occupied for 3 days by a mated adult female; and (3) predator cues, containers previously occupied by an adult female *Hogna* for 3 days. Each treatment container consisted of a 12 cm diam × 8 cm high white plastic cup with a clear lid. Before adding peat moss, all plastic cups were rinsed with 95% ethanol to remove any residual odor cues from prior use. We then placed 2 cm of commercially obtained moist peat moss in the bottom of each container. For containers requiring a stimulus, a single *Pardosa* or *Hogna* was satiated with crickets during a 24-h period, then introduced into each cup. All stimulus spiders were maintained in the cup without food for 3 days and subsequently removed. A test *Pardosa* was introduced into each of the three peat moss treatment containers (control, *Pardosa* cues, or *Hogna* cues). A different individual *Hogna* and *Pardosa* were used for each container. Every 4 days, a new set of peat moss containers was set up to maintain fresh cues for each treatment group. Immediately after transfers to new containers, test spiders were fed to satiation through ad libitum feeding within the treatment containers. Thus spiders were transferred to a new container with 3-day-old cues every 4 days and fed to excess with additional prey added every 4 days (3 times during the 14-day test period). All spiders were maintained in environmental chambers with a 13:11h light:dark photoregimen at stable humidity (50–60%) and temperature (22–25°C).

Measurement of behavior, body condition, and egg sac production. After the initial 4 days within each treatment, but before the first feeding within the stimulus containers, we measured body condition (a size-independent measure of nutritional state) for each test *Pardosa* (described in Jakob et al., 1996). Cephalothorax width and abdomen width were measured with dial calipers. Both measures were taken at the greatest width for both cephalothorax and abdomen. We used cephalothorax width as a measure of spider body size because it remains constant with food intake within an instar (Hagstrum, 1971; Jakob et al., 1996). Abdomen width increases as a function of feeding and was used as an index of body condition.

Within each treatment group, the location of the spider—on the substrate or on the side of the container—was noted, and the presence or absence of an egg sac was recorded. A spider was recorded as being on the side of the container only if all eight legs were in contact with the wall and none with the substrate. We recorded spider location three times daily at 0800, 1200, and 2100 h. Environmental chamber lighting was set on a timer. Morning recordings were completed 30 min before artificial daylight and evening recordings were recorded 30 min after artificial nightfall. Morning and evening measurements were taken using a 15-watt flashlight as the sole light source. Once egg sacs had been deposited, the spider and egg sac were removed and weighed separately on an analytical balance and then placed in 70% alcohol so that the number of eggs could be determined at a later date. We collected spiders producing egg sacs during a 14-day period, after which point the experiment was terminated. Measurement of climbing behavior was discontinued after 8 days due to a reduction in sample size from spiders producing egg sacs.

Statistical analysis. Significant differences in climbing behavior for each chemotactile cue treatment were determined with a chi-square contingency table for each time period immediately following replacement of the substrate (the mornings of day 1, day 4, and day 8). We determined differences in spider abdomen width (body condition), egg sac mass, and egg number within each treatment using one-way ANOVAs and Tukey post-hoc comparison of means tests. Data were natural-log transformed to conform to ANOVA assumptions of
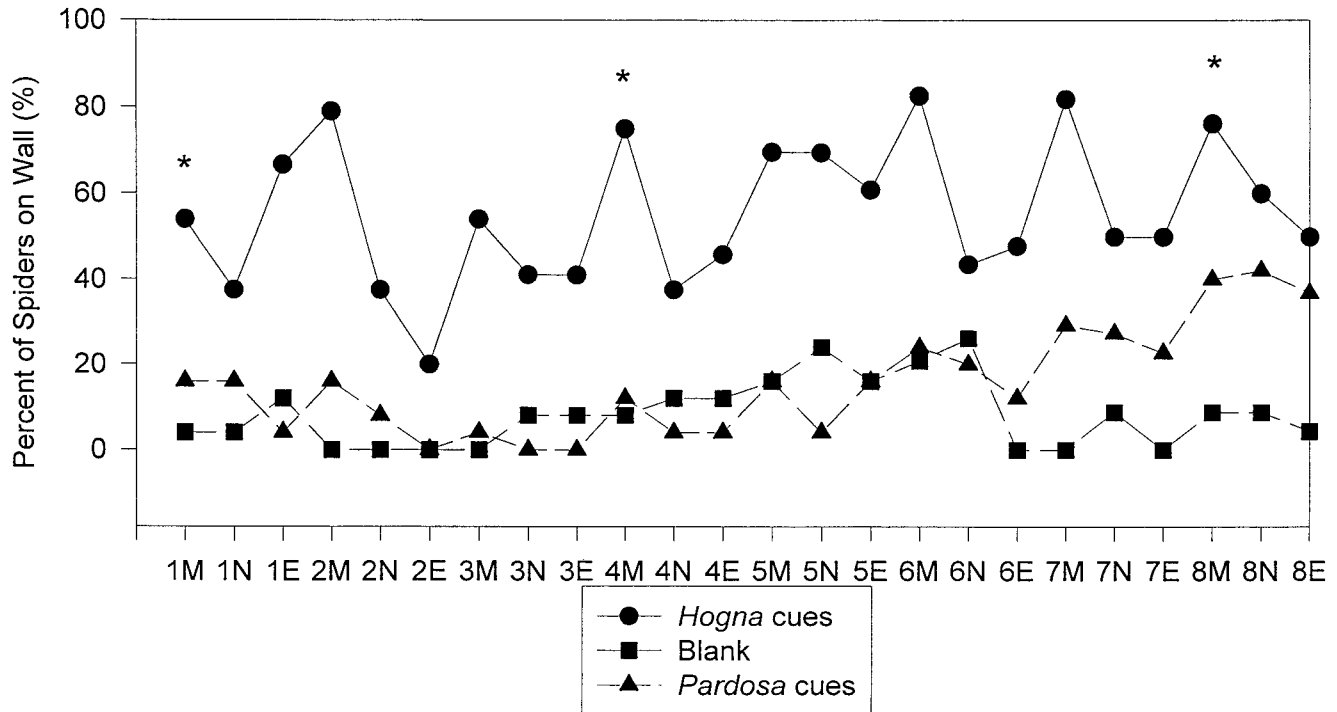
Figure 1
Percentage of spiders exhibiting climbing behavior in containers with three peat moss treatments ($n = 25$/treatment): *Hogna* predator cues present, conspecific cues present, and blank control. Spider positions were recorded over an 8-day period three times a day—morning (M), noon (N), and evening (E). Statistical differences in the number of spiders on the sides of the container were determined with a chi-square test after each time the substrate was replaced (indicated by an asterisk). Significantly more spiders were on the wall after 1 day ($\chi^2 = 19.60$, $p < .0001$), day 4 ($\chi^2 = 31.60$, $p < .00001$), and day 8 ($\chi^2 = 23.86$, $p < .00001$) in the predator cue treatments compared to other treatments.

normality when necessary. We compared differences in the number of individuals producing an egg sac within each treatment using a chi-square two-by-three contingency table. We used failure-time analysis using the Kaplan-Meier product limit estimator to compare differences in the median time to produce an egg sac, and we tested for a significant treatment effect and then compared the distribution of time to egg sac production using the log-rank (Mantel-Cox) test.

Results
Pardosa milvina exhibited significant differences in climbing behavior across the three treatment groups for each time period tested (Figure 1). Spiders spent significantly more time on the sides of the containers in the presence of *Hogna* cues than either the blank control treatment or the conspecific treatment (Figure 1), and this behavior appeared to continue over much of the 8-day recording period.

We compared cephalothorax width of spiders across treatment groups to test for the possibility that spiders differed in body size across groups by chance. Spiders were not significantly different in cephalothorax width across treatments (ANOVA, $F_{2,71} = 0.39$, $p = .68$), demonstrating that body size was not significantly different across treatments. Therefore, we used abdomen width alone rather than cephalothorax width to abdomen width ratio as an index for body condition (Jakob et al., 1996). After being maintained for 4 days, *Pardosa* exhibited significant differences in abdomen width between treatments (Table 1). Because spiders were not significantly different in cephalothorax width across treatments, this indicates a significant difference in body condition between treatments (Table 1). Tukey post-hoc comparison of means test indicated that *Pardosa* maintained in the *Hogna* cue treat-

ment had significantly smaller abdomens than either conspecific or control treatments (Table 1).

There was no significant difference in the number of egg sacs produced across treatment groups ($\chi^2 = 3.571$, $p = .167$). Spiders maintained in the *Hogna* cue treatment produced 15 egg sacs compared to 18 and 21 for control and *Pardosa* treatments, respectively. There was also no significant difference in the median time to produce an egg sac across treatment groups (Mantel-Cox test for time to egg sac production, $\chi^2 = 1.264$, df = 2, $p = .5316$; median = 12.00 ± 0.518 days for control treatment, 11.00 ± 0.414 days for *Pardosa* treatment, and $11.00 \pm$ q1.861 days for the *Hogna* treatment). However, we did find significant differences in mean egg sac weight between treatments (Table 1), with spiders from the *Hogna* treatment producing significantly lighter egg sacs than spiders in the other two treatment groups (Table 1). *Pardosa* maintained in containers with *Hogna* cues also produced significantly fewer eggs per egg sac than individuals from either of the other treatments (Table 1).

Experiment 2: effects of perceived predation risk on feeding behavior

Methods
Experiment 1 demonstrated that *Pardosa* lost weight significantly faster in the presence of *Hogna* cues than conspecific cues or blank controls. However, we were uncertain if differences in egg sac mass and egg number were due to differences in the rate of weight loss alone or if *Pardosa* also captured less prey in containers with *Hogna* cues compared to the other treatments. Therefore, we examined the effect of *Hogna* cues versus *Pardosa* cues on the feeding behavior of *Pardosa*.

Table 1

Foraging, body condition, and reproductive costs of adult female *Pardosa milvina* placed in containers previously occupied by another adult female *Pardosa*, a single predatory adult *Hogna*, or no spider (control)

	Treatment			Test statistic	p
	Control	*Pardosa* cues	*Hogna* cues		
Mean abdomen width[a] (mm)	2.50[d] ± 0.05	2.43[d] ± 0.042	2.14[e] ± 0.049	$F_{2,71} = 15.96$	.0001
Mean egg sac weight (mg)	9.21[d] ± 0.61	8.39[d,e] ± 0.54	6.62[e] ± 0.68	$F_{2,53} = 7.75$	.0011
Mean no. of eggs	21.16[d] ± 1.53	20.91[d] ± 1.331	14.13[e] ± 2.522	$F_{2,53} = 5.76$	.0055
Mean no. of flies eaten[b]		3.62 ± 0.368	1.3850 ± 0.417	$\chi^2 = 26.81$	.0001
Mean change in abdomen width[c] (mm)		0.64 ± 0.088	0.32 ± 0.110	$T_{1,24} = 2.289$	.0312

Means ± SEs are presented. See text for further details.

[a] Abdomen change as a result of 4 days in the container without food.

[b] Fruit flies eaten within 1.5 h while in each treatment.

[c] Change in abdomen width before and after exposure to fruit flies.

[d,e] Different superscript letters next to each treatment mean indicate significant differences between groups based on an ANOVA and Tukey post-hoc comparison of means test.

Stimulus preparation. We compared the number of prey consumed in 1.5 h by *Pardosa* in containers that had been previously occupied by either a *Hogna* or a conspecific ($n = 13$/treatment). Spiders were placed in opaque, colorless plastic food-service containers (5 cm high × 9 cm diam) with a 1 cm peat moss substratum. *Hogna* and *Pardosa* were fed crickets of an appropriate size once weekly before use in the experiment. The *Pardosa* were satiated, then fasted for 5 days before testing. To reduce variation in the production of *Hogna* and *Pardosa* excreta and silk, spiders to be used as stimuli for both treatments were sated with crickets 24 h before being placed in the containers. We introduced a single *Hogna* or *Pardosa* into the plastic container with a moistened peat moss substratum for 12 h. After 12 h we removed these spiders and placed a single test *Pardosa* into each container.

Measurement of feeding behavior and statistics. Five minutes after *Pardosa* were introduced, five vestigial-winged fruit flies (*Drosophila melanogaster*) were given to each spider. We then counted the number of flies consumed by each spider after 1.5 h. We compared the proportion of flies eaten between the two stimulus treatments (i.e., *Hogna* versus conspecific) using logistic regression with an indicator variable. This type of procedure is analogous to doing an ANOVA using the proper error distribution for data which consist of the number of successes/number of trials (Collet, 1991; Stokes et al., 1995). To verify that the number of prey killed was correlated with prey biomass consumed, we also tested for a change in the nutritional status of the test *Pardosa* by comparing body condition before and after the experiment. Because abdomen width is an indicator of recent foraging success (Jakob et al., 1996), we measured abdomen width of each spider before and after the experiment and calculated the change in width (width after − width before = change in abdomen width). We then compared the changes in abdomen width between treatment groups using a *t* test.

Results
Pardosa in containers that previously contained *Hogna* consumed fewer fruit flies than did spiders in containers that previously contained *Pardosa* (Table 1). *Pardosa* placed in containers with conspecific cues not only killed more fruit flies, but also consumed more prey biomass, as evidenced by an increase in abdomen width. The change in mean abdomen width was greater for spiders in containers previously occupied by *Pardosa* compared to abdomen width changes of spiders in containers previously occupied by *Hogna* (Table 1).

Experiment 3: survival value of predator chemical cue detection and climbing behavior

Methods
Because *Pardosa* behavior in the presence of *Hogna* cues is sufficient to induce weight loss, reduce feeding efficiency, reduce prey capture, and affect reproductive output, we were interested in the possible immediate survival benefits of such behavior. We tested the survival of *Pardosa* exposed to the risk of predation by *Hogna* with and without substratum-borne cues from *Hogna* and also measured survival of *Pardosa* that exhibited climbing behavior versus those spiders that did not. We collected and maintained 60 adult female *Pardosa* with egg sacs as described in experiment 1 and removed the egg sacs 24 h before testing. *Pardosa* were fed crickets until sated 12 h before to testing.

Stimulus preparation. Sixty *Hogna* were maintained in 12 cm diam × 8 cm high white plastic cups with clear lids (same containers used to house *Pardosa* in experiment 1). To standardize hunger levels, *Hogna* were sated with crickets, then fasted for 2 weeks before being used as experimental predators. We used two treatments for this experiment ($n = 30$/treatment): containers previously occupied by *Hogna* for 3 days and containers devoid of *Hogna* cues (control). *Hogna helluo* used as stimulus cues were fully satiated 24 h before introduction into the container, but were removed and replaced with a *Hogna* that had been sated then fasted for 2 weeks.

Measurement of Pardosa *survival and statistics.* After removal of the stimulus spider, but before adding the test *Pardosa* and predator, we increased heterogeneity by adding a small plastic vial wrapped in tape (4 cm long, 2.5 cm diam). Because the vial was added after the removal of the stimulus *Hogna*, it was devoid of predator silk or excreta. The vial was placed horizontally with its long axis close to the wall. The tape served to provide traction for the spider to climb on if it chose to do so. The space formed between the vial and wall was large enough to be occupied by *Pardosa*, but not *Hogna*. The opening of the vial was of a size that the predator could enter only with some difficulty. We placed a single adult, mated female *Pardosa* in each container that had an egg sac removed 24 h before the beginning of the experiment. The spider was allowed to acclimate for 1 h, after which we noted the position of the spider as being in the vial, on top of the vial, between the vial and wall on the ground, elsewhere on the ground, or on the wall exposed. Because spiders were only observed on
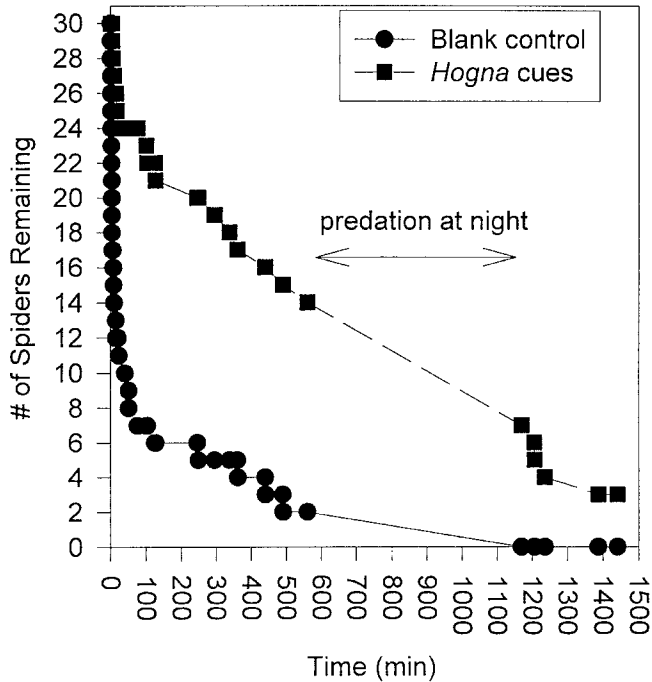
Figure 2
Number of *Pardosa* remaining alive over time in the presence of *Hogna helluo* during a 3.5-h period. Spiders either had access (*Hogna* treatment) or did not have access (blank control) to the presence of *Hogna* chemical cues during the experiment.

the wall, on top of the vial, or elsewhere on the ground, we collapsed categories to wall, vial (on top), and ground. A single *Hogna* was introduced into the container at noon. Each container was monitored continuously for a 1 h period, every 5 min for the second and third hour, and once every 30 min thereafter for a 24-h period. Observations were suspended at 2200 h, and the room lighting was turned off and resumed at 0800 h when lighting was again turned on the next day. To compare the effectiveness of various *Pardosa* positions in the

container as possible predator deterrents, we recorded the positions of spiders killed within the first 5 min of the experiment.

To analyze the effectiveness of being in a vertical position in deterring predation, we compared differences in *Pardosa* predation latency across peat moss treatments based on both the position of *Pardosa* and the presence of *Hogna* cues. We compared differences in the median time of predation by *Hogna* for each treatment using a Kaplan-Meier failure time analysis (log-rank test). Differences in space use in the container were tested using a chi-square test.

Results
Pardosa milvina survived much longer in the presence of *Hogna* chemotactile cues than in containers lacking such cues. Based on a Kaplan-Meier failure-time analysis, there was a highly significant difference in the median time to predation between *Hogna* and control treatments (log-rank test, $\chi^2 = 26.96$, df = 1; $p < .0001$; Figure 2). *Pardosa* survived a median of only 8.83 ± 1.96 min in the container without substratum-borne cues from *Hogna,* but survived a median of 9.34 ± 0.709 h when *Hogna* cues were present.

Pardosa showed a significant difference in their initial positions in the containers with or without predator chemotactile cues ($\chi^2 = 21.86$, $p < .0009$; Figure 3A). In containers without *Hogna* cues, most spiders were found resting on the top of the vial, with fewer on the ground, and the fewest number positioned vertically on the wall (Figure 3A). In the *Hogna* treatment, the majority of spiders were occupying the wall with equal numbers on the ground or vial top (Figure 3A). After the first 5 min of introducing the predator, there were significant differences in survival of spiders based on their position within the container ($\chi^2 = 32.80$, $p < .0001$, $n = 23$). All *Pardosa* that were vertically oriented on the walls survived, whereas only 4 out of 19 spiders on the vial and 6 out of 14 spiders on the ground survived (Figure 3B). Chemotactile cues from predators elicit climbing behavior, but vertical positions in the container are not favored by *Pardosa* when predators are not present (Figure 3A). The vertical orientation of *Pardosa* did significantly reduce predation by *Hogna* (Figure 3B).
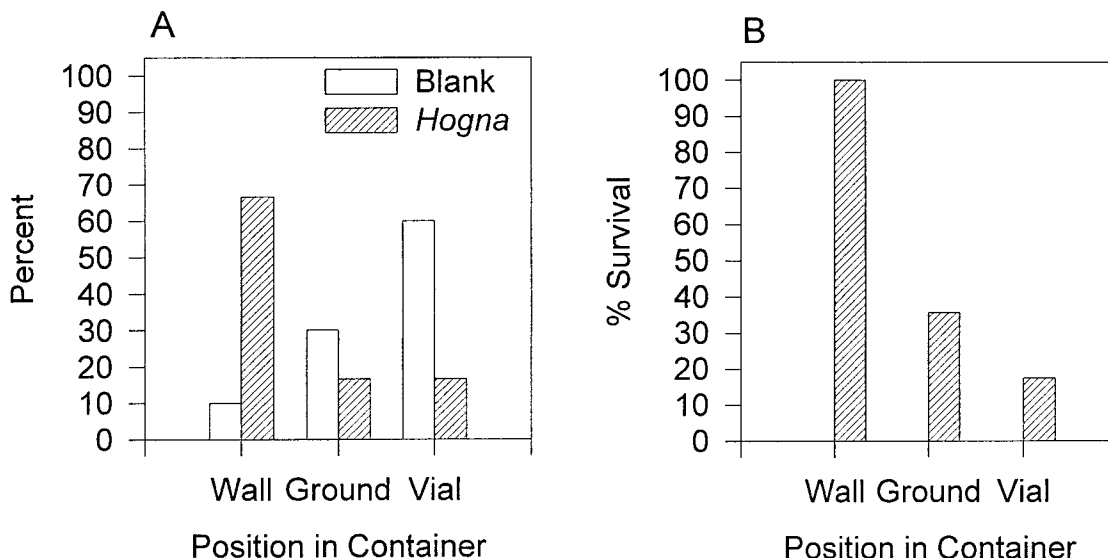

Figure 3
(A) Differences in space use among *Pardosa* in the presence of *Hogna* cues or blank control containers. Percentage of *Pardosa* on the sides of the container (wall), ground, or on top of a vial. (B) Percentage of *Pardosa* that survived *Hogna* predation while occupying the wall, ground, or top of vial in the container.

Hogna were found to engage in nocturnal foraging because they preyed on *Pardosa* in nearly complete darkness between 2200 and 0800 h (Figure 2). During this time, nine *Pardosa* were captured and eaten in the absence of a light source. This indicates that *Hogna* probably located *Pardosa* through vibratory, tactile, and/or chemical cues.

DISCUSSION

Fitness-related costs due to chemically induced antipredator behavior have been commonly found within aquatic systems (Chivers and Smith, 1998), but far fewer analogous studies have been conducted in terrestrial systems. Further, although many shifts in behavior have been documented in the presence of either an actual predator or indirect cues associated with a predator, few studies document if such changes in behavior actually result in reduced predation when the predator is present (Persons et al., 2001; Venzon et al., 2000). Here we document the occurrence of behavioral changes by prey due to chemotactile cues from predators in a terrestrial arthropod. We also document that although there are significant fitness-related costs to this shift in space use, it is also an extremely effective antipredator behavior against the *Hogna* producing the cues.

Our results suggest that climbing behavior is both energetically costly and reduces prey capture efficiency. Spiders in experiment 1 were fed before initial introduction into each treatment and were measured before a second feeding. Measurements indicate that *Pardosa* were losing weight more quickly in containers that previously contained *Hogna*. The difference in weight loss could be attributed to physiological costs borne by the stress of being under constant perceived predation risk and therefore may be independent of whether spiders were exhibiting climbing behavior. However, the majority of spiders climbed the sides of the container in the *Hogna* treatment, unlike their behavior in the other treatment, which suggests a larger energetic cost associated with maintaining a position on the side of the container rather than the ground. Minimally, results indicate that the spider's preferred location is not on the side of the container. Wolf spiders are generally ground dwellers (Lowrie, 1968), and, unlike other ground-dwelling spiders such as gnaphosids, clubionids, and corinnids, wolf spiders lack scopular hairs on the most distal portion of the leg. Scopular hairs aid in adhering to smooth surfaces (Foelix, 1996). Even lycosid species such as *Rabidosa rabida* that typically are found in herbaceous vegetation seem to prefer horizontal or gently sloping surfaces on plants (Rovner and Knost, 1974). *Pardosa* lack scopular hairs at the tips of their tarsi and were observed to have some difficulty climbing the sides of the plastic containers.

The energetic costs of climbing behavior are compounded by the fact that the presence of predator cues either inhibits feeding behavior or reduces capture success. The feeding experiment indicates that spiders not only kill fewer prey, but also eat fewer prey when in the presence of chemotactile cues from a predator than in the presence of conspecific cues. There are a number of nonmutually exclusive reasons that *Pardosa* may exhibit reduced fruit fly predation in the containers with *Hogna* cues. Spiders may have had difficulty capturing prey because they were residing on the side of the container and therefore used their legs for maintaining their position rather than lunging at prey. *Pardosa* that do lunge at prey while on the side of the container are probably more likely to drop to the ground, which, as our data show, is a more dangerous place to be if a *Hogna* is present. *Pardosa* may have shown a decrease in activity in the container with *Hogna* cues. Previous studies indicate that *Pardosa* reduce activity levels in the presence of *Hogna* chemotactile cues and

that such behavior has a survival benefit (Persons et al., 2001). Decreased movement would have a negative impact on prey capture.

Increased energetic costs and the decreased foraging efficiency that results from residing in the presence of *Hogna* cues may have both contributed to reduced reproductive output. Spiders in the presence of *Hogna* cues produced fewer (though not significantly fewer) egg sacs than spiders in either conspecific or control treatments. *Pardosa* produced significantly lighter egg sacs and fewer eggs when exposed to predator cues for 2 weeks. We found no evidence that predator cues affect the latency to produce an egg sac, suggesting that the presence of *Hogna* chemical cues is not likely to have a large impact on the phenology of *Pardosa*. However, the presence of large numbers of predators could have a significant impact on *Pardosa* populations even if actual predation seldom occurs.

Although the reproductive and foraging costs for climbing behavior are high, the survival benefit of climbing may also be high. Spiders that climbed the sides of the container had 100% survival compared to individuals on the ground (42%) or vial top (21%) (Figure 3B). Climbing behavior appeared to be mediated primarily, if not exclusively, by the presence of *Hogna* cues on the substrate. Although *Pardosa* could presumably detect *Hogna* in the container through tactile cues, visual cues, vibratory cues through the substratum, and/or possibly even airborne volatiles, these sensory channels combined were insufficient to elicit high levels of climbing behavior. This suggests that detection of substratum-borne predator cues by the prey is the primary means of predator detection and is extremely important for survival in a *Hogna–Pardosa* encounter.

It is likely that the field equivalent to climbing behavior may be either avoidance of the substrate or moving into the nearest available patch of vertical vegetation. Adult *Pardosa* will avoid substrates containing *Hogna* silk and excreta (Persons et al., 2001). However, we suggest that simple avoidance of the substrates containing predator cues does not fully explain observed climbing behavior. *Pardosa* did not climb on the vial top, which was both devoid of cues and horizontally oriented when *Hogna* cues were present on the peat moss. This indicates that *Pardosa* did not climb the walls and assume a vertical orientation only to avoid direct contact with *Hogna* cues, but rather that vertical orientation may deter prey capture by *Hogna*. Under natural conditions, it is unknown if *Pardosa* will exhibit climbing behavior on the nearest vegetation when encountering *Hogna* silk or excreta. Previous studies show that *Pardosa* may show other effective defensive behaviors in the presence of *Hogna* as well such as avoidance and decreased activity (Persons et al., 2001). During our collection of *Hogna* and *Pardosa,* we did observe that *Pardosa* could be found in large numbers in soybean plants and high in vegetation on some occasions, and strictly found on the ground at other times. The cause for this shift in space use is currently unknown, but this study suggests that predator avoidance cannot be ruled out as an explanation.

Our results are important in understanding predator–prey dynamics among these two species. This study confirms the results of other experiments that suggest that chemotactile cues alone induce antipredator behavior, not the predator itself (Persons et al., 2001). Also, *Pardosa* are capable of fine discrimination between predators that pose different levels of predation risk. Spiders show graded levels of activity depending on the diet of the *Hogna* (Persons et al., 2001) producing the cues. In light of our finding that defensive behaviors incur significant fitness costs, exhibition of graded responses to different levels of perceived risk may be a means of mitigating these costs. Other studies suggest that indirectly mediated

predator–prey interactions are much more common in ground-dwelling spiders than previously realized. Punzo (1997) found that wolf spiders *Schizocosa avida* showed increased avoidance of substrates previously occupied by the scorpion *Centruroides vittatus* if they had been previously attacked by the scorpion than if they had never encountered it. Wolf spiders may use chemotactile cues to locate prey more efficiently as well. Persons and Uetz (1996) found that the wolf spider *Schizocosa ocreata* spends longer periods of time on substrates previously occupied by house crickets compared to controls. Punzo and Kukoyi (1996) found that the wolf spider *Trochosa parthensus* and the oxyopid *Oxyopes salticus* spend longer periods of time on substrates previously occupied by prey common to their natural habitat compared to cues from novel prey. Persons and Rypstra (2000) found that *H. helluo* prefer substrates previously occupied by their most recent prey and also show attraction to chemotactile cues from *Pardosa* when fed *Pardosa*.

These results clearly show that chemotactile detection of predators is critical for spiders to perform effective defensive behavior and that both the costs and benefits of climbing behavior are high. Spiders tended to remain on the sides of the containers for the entire time that *Hogna* cues were present, even when the actual predator was absent. This suggests that *Pardosa* may tend to overestimate predation risk and weigh the benefits of climbing behavior more heavily than the reproductive and feeding costs incurred by it. Selection pressure for *Pardosa* to respond to indirect predator cues is likely to be high. Future field studies will be necessary to verify the adaptive significance of chemotactilely mediated shifts in space use.

REFERENCES

Barry MJ, 1994. The costs of crest induction for *Daphnia carinata*. Oecologia 97:278–288.

Brown GE, Chivers DP, Smith RJF, 1995. Fathead minnows avoid conspecific and heterospecific alarm pheromones in the faeces of northern pike. J Fish Biol 47:387–393.

Chivers DP, Smith RJF, 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. Ecoscience 5:338–352.

Collet D, 1991. Modelling binary data. New York: Chapman and Hall.

Crowl TA, Covich AP, 1990. Predator-induced life-history shifts in a freshwater snail. Science 247:949–951.

Dondale CD, Redner JH, 1990. The insects and arachnids of Canada. Part 17: The wolf spiders, nurseryweb spiders, and lynx spiders of Canada and Alaska. Ottawa, Ontario: Agriculture Canada.

Edgar WD, 1971. Seasonal weight changes, age structure, natality and mortality in the wolf spider *Pardosa lugubris* Walck in central Scotland. Oikos 22:84–92.

Foelix RF, 1996. Biology of spiders. New York: Oxford University Press.

Gore RH, 1966. Observations on the escape response of *Nassarius vibex* (Say) (Mollusca: Gastropoda). Bull Mar Sci 16:423–434.

Grostal P, Dicke M, 1999. Direct and indirect cues of predation risk influence behavior and reproduction of prey: a case for acarine interactions. Behav Ecol 10:422–427.

Hagstrum D, 1971. Carapace width as a tool for evaluating the rate of development of spiders in the laboratory and field. Ann Entomol Soc Am 64:757–760.

Hoffmeister TS, Roitberg BD, 1997. Counterespionage in an insect herbivore-parasitoid system. Naturwissenschaften 84:117–119.

Holomuzki JR, Short TM, 1990. Ontogenetic shifts in habitat use and activity in a stream-dwelling isopod. Holarct Ecol 13:300–307.

Jakob EM, Marshall SD, Uetz GW, 1996. Estimating fitness: a comparison of body condition indices. Oikos 77:61–67.

Kats LB, Dill LM, 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Ecoscience 5:361–394.

Kats LB, Petranka JW, Sih A, 1988. Antipredator defenses and the persistence of amphibian larvae with fishes. Ecology 69:1865–1870.

Koskela E, Ylönen H, 1995. Suppressed feeding in the field vole (*Microtus agrestis*): an adaptation to cyclically fluctuating predation risk. Behav Ecol 6:311–315.

Lima SL, 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv Study Behav 27:215–290.

Lima SL, Dill LM, 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can J Zool 68:619–640.

Lowrie DC, 1968. The spiders of the herbaceous stratum of the Jackson Hole region of Wyoming. Northwest Sci 42:89–100.

Magnhagen C, 1991. Predation risk as a cost of reproduction. Trends Ecol Evol 6:183–186.

Malmqvist B, 1992. Stream grazer responses to predator odour: an experimental study. Nord J Freshw Res 67:27–34.

Marshall SD, Gittleman JL, 1994. Clutch size in spiders: is more better? Funct Ecol 8:118–124.

Marshall SD, Rypstra AL, 1999. Patterns in the distribution of two wolf spiders. Environ Entomol 28:1052–1059.

Persons MH, Uetz GW, 1996. Wolf spiders vary patch residence time in the presence of chemical cues from prey (Araneae, Lycosidae). J Arachnol 24:76–79.

Persons MH, Rypstra AL, 2000. Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). Ethology 106:27–35.

Persons MH, Walker SE, Rypstra AL, Marshall, 2001. Wolf spider responses and survival in the presence of diet-associated predator cues. Anim Behav 61:43–51.

Punzo F, 1997. Leg autotomy and avoidance behavior in response to a predator in the wolf spider, *Schizocosa avida* (Araneae, Lycosidae). J Arachnol 25:202–205.

Punzo F, Kukoyi O, 1997. The effects of prey chemical cues on patch residence time in the wolf spider *Trochosa parthenus* (Chamberlin) (Lycosidae) and the lynx spider *Oxyopes salticus* Hentz (Oxyopidae). Bull Br Arachnol Soc 10:323–326.

Repka S, Ketola M, Walls M, 1994. Specificity of predator-induced neck spine and alteration in life history traits in *Daphnia pulex*. Hydrobiologia 294:129–140.

Rovner JS, Knost SJ, 1974. Post-immobilization wrapping of prey by lycosid spiders of the herbaceous stratum. Psyche 81:398–415.

Spitze K, 1992. Predator-mediated plasticity of prey life-history and morphology: *Chaoborus americanus* predation on *Daphnia pulex*. Am Nat 139:229–247.

Stokes M, Davis C, Koch G, 1995. Categorical data analysis using the SAS system. Cary, North Carolina: SAS Institute.

Sweitzer RA, Berger J, 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology 73:867–875.

Venzon M, Janssen A, Pallini A, Sabelis MW, 2000. Diet of a polyphagous arthropod predator affects refuge seeking of its thrips prey. Anim Behav 60:369–375.

Wahle RA, 1992. Body-size dependent anti-predator mechanisms of the American lobster. Oikos 65:52–60.

Ylönen H, Ronkainen H, 1994. Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. Evol Ecol 8:1–9.

Young O, Edwards E, 1990. Spiders in United States field crops and their potential effect on crop pests. J Arachnol 18:1–27.