



Tradeoffs involved in site selection and foraging in a wolf spider: effects of substrate structure and predation risk

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Understanding how animals weigh habitat features, exposure to predators and access to resources is important to determining their life history and distribution across the landscape. For example, when predators accumulate in structurally complex habitats, they face an environment with different competitive interactions, foraging opportunities and predatory risks. The wolf spider *Pardosa milvina* inhabits the soil surface of highly disturbed habitats such as agricultural fields throughout eastern North America. *Pardosa* displays effective antipredator behavior in the presence of chemical cues produced by a larger coexisting wolf spider, *Hogna helluo*. We used those cues to simulate predation risk in laboratory and field experiments designed to test the effects of habitat substrate and predation risk on site selection and prey consumption of *Pardosa*. In general, *Pardosa* preferred more complex substrates over bare dirt but those preferences were eliminated or reversed when cues from *Hogna* were present. Feeding trials revealed that substrate alone had few effects on *Pardosa* prey consumption, which we measured by documenting the change in the abdomen width. Although the presence of *Hogna* cues reduced prey consumption overall in field feeding trials, the negative effect of predation risk on prey consumption was only observed in grass and bare dirt substrates in the laboratory. We also found that prey capture was negatively affected by habitat complexity for both spider species but that same complexity offered *Pardosa* protection from predation by *Hogna*. This study provides insight into how two predator species interact to balance site selection and feeding in order to avoid predation. Shifts in foraging and distributional patterns of predators can have profound implications for their role in the food web.

Habitat selection has profound consequences for animals, affecting foraging success, reproduction and survival. However, site selection is complicated by the fact that optimal habitat features for different activities do not necessarily co-occur and animals are forced to weigh the costs and benefits as they prioritize one potential outcome over another. For example, habitats that enable an animal to locate potential mates and food may also be habitats where the animal is at risk of being attacked by predators (Werner et al. 1985, Heck and Crowder 1991, Brown 1999, Brown et al. 1999, Schofield 2003). Recently it has been proposed that we view animal distribution and behavior in two landscapes, one defined by the basic needs of the organism such as food and shelter and the second reflecting differing levels of predation risk (Laundré

et al. 2001, Hernandez and Laundré 2005, Schmitz 2005). This second “landscape of fear” takes into account the fact that predator information can shift habitat use, affect activity, increase vigilance and/or reduce foraging of potential prey. These ideas have been useful in understanding the distribution of vertebrate herbivores in the face of predators (Laundré et al. 2001, Hernandez and Laundré 2005, Schmitz 2005), however it is also critical to consider how this second landscape might influence the distribution of different species of predators as well as their mutual prey.

Spiders are common predators in terrestrial ecosystems that have strong influences on the food web (Schmitz et al. 2000, Halaj and Wise 2001). Since they are cannibals and intraguild predators that depend on the same food base, their landscape of fear is

complicated by inter- and intra-specific interactions. Spider abundance and diversity are associated with habitat structural complexity and wolf spiders in particular tend to accumulate in areas where mulch or plant debris has collected on the soil surface (Rypstra et al. 1999, Langellotto and Denno 2004). Although reduced predation, increased prey capture success and/or improved microclimate conditions have most frequently been suggested to explain these habitat connections, few studies have attempted to link multiple habitat features or explored the various tradeoffs a given population might experience as they move across a complex landscape (Uetz 1991, Rypstra et al. 1999, Finke and Denno 2002, Langellotto and Denno 2004). With the goal of understanding how the density and distribution of spiders might reflect a landscape of fear, we explored site selection and foraging of a generalist wolf spider and determined how these activities were affected by predation risk. Ultimately, by combining space use, foraging and predation risk in experiments we will be able to make predictions about the distribution, density and prey consumption patterns of the spider community and better understand their role in terrestrial food webs.

The wolf spider *Pardosa milvina* (Araneae, Lycosidae) (hereafter referred to as *Pardosa*) is one of the most common spider species on the soil surface of agricultural fields in eastern North America (Dondale and Redner 1990, Young and Edwards 1990, Marshall and Rypstra 1999). *Pardosa* individuals are particularly abundant in disturbed habitats where they accumulate in patches of mulch or other debris on the soil surface (Marshall and Rypstra 1999, Marshall et al. 2000, 2006). *Pardosa* is a small species (20–30 mg) that regularly coexists with a much larger wolf spider, *Hogna helluo* (Araneae, Lycosidae, hereafter referred to as *Hogna*, 400–500 mg) (Marshall et al. 2000, 2006). Although *Pardosa* readily consume juvenile *Hogna*, the large size differential between adults makes *Pardosa* a common prey item for adult *Hogna*, which are 20 times their size (Balfour et al. 2003, Rypstra and Samu 2005). Presumably because *Hogna* is such a ubiquitous threat, *Pardosa* has evolved the ability to detect chemotactile cues (silk and excreta) that *Hogna* deposits as it occupies an area (Persons et al. 2001, 2002). The behavioral reactions of *Pardosa* to *Hogna* cues are commensurate with the risk posed; they detect the size (Persons and Rypstra 2001), sex (Lehmann et al. 2004), hunger level (Bell et al. 2006), and diet (Persons et al. 2001) of the *Hogna* that produced the cues and shift their behavior in ways that increase their survival when the predatory *Hogna* is present. The efficacy of *Hogna* cues fades with time (Barnes et al. 2002) and exposure to the elements (Wilder et al. 2005) and so the cues provide *Pardosa* with accurate information as to the imminence of the threat. Here we use *Hogna*'s chemotactile cues to

explore how the knowledge that a predator is present affects the habitat selection and foraging decisions of *Pardosa*.

The goal of this study was to develop an understanding of how *Pardosa* interacts with their physical landscape and how that interaction is altered by the landscape of fear. In a series of laboratory and field experiments, we documented preferences of *Pardosa* for specific habitat substrates and quantified their ability to function on those substrates by quantifying prey consumption. We then examined the shifts in the habitat preferences and prey consumption of *Pardosa* in the presence of predator information (i.e. cues from *Hogna*). Finally we monitored prey capture by *Pardosa* and *Hogna* in two contrasting habitat substrates and specifically how the prey capture by *Pardosa* was influenced by the presence of the actual predator.

Methods

Pardosa milvina were collected from soybean and cornfields at Miami Univ. Ecology Research Center (Oxford, Butler County, OH) between May and August 2000, 2001 and 2004. The predators in our experiments, *Hogna helluo*, were collected from the same site or reared in the laboratory from the egg sacs of field caught adult females. When not used in experiments, *Pardosa* were housed in 150 ml containers and *Hogna* were housed in 450 ml containers with a layer of damp peat moss on the base to provide substrate and moisture. Containers were kept in an environmental chamber at 23°C on a 13:11 L: D cycle. Twice a week the peat moss was watered and the spiders were fed two crickets (*Acheta domesticus*), each approximately half the size of the spider. Only adult female *Pardosa* and *Hogna* without egg sacs were used in experiments. In order to ensure that the *Hogna* used in predator cue trials would produce similar amounts of silk and excreta, we provided them with an abundance of crickets and allowed them to feed ad libitum for 24 h before we used them to deposit chemotactile cues for an experiment. We made morphological measurements of the spiders (carapace and abdomen width) to the nearest 0.01 mm using an ocular micrometer on a Wild M5 Heerbrugg stereomicroscope.

Both laboratory containers and field enclosures used were washed thoroughly and allowed to dry between each use. Substrates used in laboratory trials were autoclaved prior to use to remove all extraneous cues. Prior to and after installation of the field enclosures, we searched the inside area carefully and removed all spiders and other arthropod predators. Substrates were then added, watered and left for 3–7 d to ensure that any residual *Hogna* cues would have dissipated (Barnes et al. 2002, Wilder et al. 2005). We moved the field

enclosures to new locations between experimental trials. In all cases, the soil and habitat substrates were discarded after one use. Each time experimental trials were conducted, we included the same number of representatives of each treatment so as to control for any effects of timing or, in the case of field trials, weather. No spider was used more than once. All statistical analyses were performed using JMP 5.1 (Anonymous 2005).

Habitat choice

Laboratory experiment

To determine their habitat preferences in the laboratory, *Pardosa* were given the choice of occupying two distinct habitat substrates. Experiments were run between June and October of 2000 and 2001 in aquaria measuring 26 × 50 cm with 30 cm walls. A layer of smooth hard packed dirt covered the bottom and any additional substrate was added on top to form an additional 2–3 cm layer. Four habitats used in these trials were: bare dirt, fresh cut grass, wheat straw and dead maple leaves (mostly *Acer rubrum* with some *A. saccharum*). Each substrate covered a 22 × 26 cm area at opposite ends of the aquaria. A 6 × 26 cm transition zone of bare dirt was left in the middle section to separate the two options. We tested all substrate pairings: dirt vs grass, dirt vs straw, dirt vs leaves, grass vs straw, grass vs leaves and straw vs leaves. Since *Pardosa* were observed to prefer grass over bare dirt in preliminary trials, we also tested this pairing with *Hogna* cues deposited on the grass. In order to prepare the cue treatment, a divider was placed between the two substrates and one *Hogna* was confined to the area where the grass was located for 24 h. The divider and *Hogna* were removed just before the trial was to begin.

Adult female *Pardosa* were assigned to treatments and paired randomly. One member of each pair was marked with a drop of non-toxic paint on the dorsal surface of the abdomen so that individuals could be identified. We fed each *Pardosa* two 10 mg crickets 24 h prior to the beginning of the experiment. At 08:30 h on the first day, they were released into the transition zone of the aquarium. We recorded the substrate in which we found each *Pardosa* twice daily at 08:30 and 20:30 h for seven days. If a spider was located in the transition zone, the observation was not counted. A total of ten replicates of each treatment were run. We summed the number of observations in a given habitat for each individual spider to generate a preference score. Since we could not assume that the spiders in the same aquarium were acting independently, we took the mean of the scores for the two animals in the same aquarium to generate one preference score for each habitat in each

replicate. Since we had no a priori predictions about their preferences, we took the absolute value of the difference between the two preference scores for a given substrate pairing and used that as an indication of habitat choice. These choice scores were compared across treatments using one-way ANOVA and Tukey post-hoc tests.

Field experiment

Additional habitat choice trials were run in field enclosures between June and September 2000 at Miami Univ. Ecology Research Center (5 km north of Oxford, Butler County, OH, USA). We constructed 1 m² circular enclosures of 40 cm aluminum of which 5 cm were buried into the ground. The top 2 cm was bent toward the center to prevent *Pardosa* from escaping. Three substrates were used in field trials: bare dirt, live grass and plant debris, which was comprised of a 2–3 cm layer of leaves, grass clippings and straw placed on top of well packed dirt. The choices for the field experiments included all possible combinations of the three substrates (dirt vs grass, dirt vs plant debris, grass vs plant debris). The substrates covered a little less than half of the enclosure with a five cm transition zone of exposed dirt across the middle. Ten replicates of each combination were tested with and without predator cues. For trials with predator cues, two satiated *Hogna* females were released in the arena 24 h prior to the trial and removed immediately before the *Pardosa* were introduced. We did not try to confine the *Hogna* to any particular substrate but rather let them roam freely to find their preferred habitat during the cue deposition period and recorded their habitat selection when we removed them. In cases where *Hogna* were not all found in the same substrate, we compared their habitat selection using Fisher's exact probability test.

Adult female *Pardosa* were randomly assigned to treatments in groups of five and marked individually with a dot of non-toxic paint. Each *Pardosa* was fed two 10 mg crickets and allowed 24 h to consume them. We then released the five individuals into the transition zone of an enclosure. After three days, we thoroughly searched the enclosures and recorded the substrate selected by each spider. We determined if treatment or the presence of *Hogna* cues affected *Pardosa* survival using the Cochran-Mantel-Haenszel test. To quantify habitat selection, we created preference scores by calculating the percent of spiders found in each habitat substrate in each enclosure. We calculated choice scores for the treatments with no predator information by subtracting the score for the less preferred habitat (lower preference score) from the score for the more preferred habitat (higher preference score). Since we were looking for a shift in habitat use in the presence of predator

cues, we calculated the choice scores for predator treatments using the habitat priorities from the treatments with no predator cues (i.e. score for the preferred habitat in the predator free treatments minus the score for the less preferred habitat in the predator free treatments). Choice scores were compared across treatments in a two-way ANOVA with substrate pair and cues as factors. Specific pairwise comparisons were conducted with the Tukey post-hoc tests.

Prey consumption

Since spiders are typically food limited in nature (Wise 1993, 2006), we elected to use prey consumption as an indicator of how habitat substrate and predator information affect the ability of *Pardosa* to function in a given environment. Typically, body measurements are used to quantify body condition and/or hunger of spiders in the laboratory and field (Nakamura 1968, 1972, Anderson 1974, Jakob et al. 1996, Walker et al. 1999, Marshall et al. 2000, McNett and Rypstra 2000, Persons et al. 2002). In particular, the carapace width, tibia length or some other measure of an inflexible part of the exoskeleton is used as a measure of absolute body size since it can only change at molt. However, abdomen of spiders is flexible and changes in size as the spider feeds. Thus, the size of the abdomen relative to the carapace can be used to assess overall hunger level of field populations and any change in the size of the abdomen of an individual is a reflection of recent prey consumption (Nakamura 1968, 1972, Anderson 1974, Givens 1978, Jakob et al. 1996, McNett and Rypstra 2000, Persons et al. 2002, Moya-Laraño et al. 2003).

Laboratory experiment

Laboratory experiments were conducted in aquaria, each measuring 26 × 50 cm, between July and September 2000 and 2001. The bottom of each aquarium was covered with smoothed packed dirt and, for some treatments, 2–3 cm of fresh cut grass, straw, or dead maple leaves were added to cover the entire area. Prey consumption of *Pardosa* was quantified in all four substrates with and without predator cues. For treatments with predator cues, an adult female *Hogna* was placed in the aquarium to deposit chemical cues for 24 h and then removed. To standardize hunger, each *Pardosa* was fed two 10 mg crickets and then held with water but no food for two days. At the commencement of the experiment, eight 10 mg crickets were released into each aquarium and allowed two hours to establish themselves before the introduction of *Pardosa*. We assigned *Pardosa* to treatments and paired them randomly. We marked one member of each pair with

a dot of non-toxic paint on the dorsal surface of the abdomen. We measured the carapace width and abdomen width of each *Pardosa* just before we released them and again after 24 h of foraging. A total of 10 replicates were run for each treatment with and without predator cues.

In order to verify that the animals placed in different treatments were similar in size and body condition, we compared the carapace and abdomen measurements of all animals using one-way ANOVAs. We estimated the consumption of each individual by taking the difference between the abdomen measurements before and after they were allowed to forage in a given substrate. Because animals in the same aquarium at the same time could not be considered independent, we compared the mean abdomen change of the two spiders in each aquarium using a two-way ANOVA with habitat substrate and predator cues as factors. Specific pairwise comparisons were conducted with the Tukey post-hoc tests.

Field experiments

The effects of habitat and predator cues on *Pardosa* prey consumption were also quantified in field enclosures. We conducted these trials during July–September 2000 in 1 m² circular enclosures similar to those used in habitat choice experiments. In this situation, the bottom of the entire enclosure was covered with a single substrate (dirt, grass or plant debris). For cue treatments, two *Hogna* were introduced 30 h prior to experimentation and removed after 24 h. Ten crickets, 10 mg in size, were released into each enclosure 6 h prior to *Pardosa* introduction.

We randomly assigned *Pardosa* to treatments in groups of five and marked each member of the group individually with a dot of non-toxic paint. Seventy-two hours prior to the beginning of the experiment, each *Pardosa* was provided with two 10 mg crickets and allowed to forage for 24 h. They were then held with water but no food for 48 h. The day of the experiment, we measured carapace width and abdomen width and released them into their designated enclosure. After three days, we thoroughly searched the enclosures for *Pardosa* and remeasured all those that we were able to capture. A total of 10 replicates were run in each habitat with and without predator cues.

In order to verify that the animals placed in different treatments were similar in size and body condition, we compared the carapace and abdomen measurements taken before the experiment using one-way ANOVAs. The effects of habitat substrate and predator cues on our ability to recover *Pardosa* were evaluated using the Cochran-Mantel-Haenszel test. The change in abdomen width was calculated for each spider recovered. Since we could not assume that the consumption of

spiders in the same enclosure was independent, we averaged the abdomen width change of the recovered animals in each enclosure. The effects of substrate and predator cues on the mean abdomen width change, our measure of prey consumption, were assessed in a two-way ANOVA. Specific pairwise comparisons were conducted with the Tukey post-hoc tests.

Prey capture of *Pardosa* and *Hogna*

In order to further establish the effects of substrate complexity on the ability of *Pardosa* to capture prey (as opposed to prey consumption as quantified above) and to determine how the actual presence of *Hogna* might interfere with prey capture, we conducted a second laboratory experiment in July-August 2004. In this experiment we allowed *Pardosa* and *Hogna* to capture prey separately and together on two contrasting substrates: bare dirt and dirt with straw added. These trials were run in cylindrical plastic containers, 20 cm in diameter with 7.5 cm walls. A layer of bare dirt covered the bottom of all the containers and a 2–3 cm layer of straw was added to half of them. Seven days before the experiment, we provided *Pardosa* with as many 10 mg crickets as they would kill and consume in a 24 h period and then we held them with water but no food until the day of the experiment. To minimize mortality of *Pardosa* in trials with both spider species, we fed each *Hogna* two 15 mg crickets 24 h before trials.

At the commencement of a trial, ten 10 mg crickets were introduced into each container and allowed five minutes to establish themselves. In the single spider treatments, we placed the experimental animal, either a *Pardosa* or *Hogna*, in the center of the container under a glass vial and allowed it to acclimate for five minutes before we released it. At the beginning of the treatment with both spiders, we released the *Pardosa* first, allowed it five minutes to acclimate and then introduced the *Hogna* in the same manner. After two hours, we removed the spiders and counted the remaining crickets. The carapace width and abdomen width of all *Pardosa* were measured just before and after the

foraging bout. A total of 20 replicates were run in each habitat with and without the presence of *Hogna*.

To assess any size biases in the assignment of *Pardosa* to treatments, we compared the carapace width and initial abdomen width across treatments in one-way ANOVAs. The number of crickets remaining and the change in abdomen width of *Pardosa* over the two hours were compared across treatments in a two-way ANOVA with habitat substrate and spider combination as factors. Specific pairwise comparisons were conducted with the Tukey post-hoc test. For those treatments that included both spider species, we compared the number of *Pardosa* killed by *Hogna* in the two substrate treatments using Fisher's exact probability test.

Results

Habitat choice

Laboratory experiment

Choice scores revealed that *Pardosa* discriminated among the various habitat substrates ($F = 7.32$, $DF = 6$, $p < 0.0001$, Table 1). Habitat preferences were most distinct when *Pardosa* were given the option of inhabiting grass as opposed to bare dirt (Table 1). Although not significantly different from those of straw vs dirt, the choice scores for grass vs dirt were different from all other pairings (Table 1). Predator cues deposited on grass eliminated *Pardosa*'s preference for that habitat over bare dirt (Table 1).

Field experiment

We recovered all of the *Hogna* used for predator cues after their 24 h in field enclosures. All *Hogna* were found in the grass or plant debris when those substrates were paired with bare dirt but they did not show a preference for grass (12 of 20) when it was paired with plant debris (8 of 20, Fisher exact probability test, $p = 0.34$). There was no effect of substrate or predator cues on our ability to recover *Pardosa* in field enclosures after three days (Cochran-Mantel-Haenszel test:

Table 1. The mean preference scores (\pm SE) calculated for each habitat and the choice score for each pairing in the laboratory habitat choice experiment. Choices scores indicated with the different letters were significantly different using Tukey post-hoc test ($p < 0.05$).

Substrate 1	Preference score	Substrate 2	Preference score	Choice score	
Leaves	6.4 \pm 3.6	grass	7.6 \pm 3.6	0.5 \pm 2.1	A
Leaves	6.3 \pm 2.9	straw	7.7 \pm 2.9	0.8 \pm 1.1	A B
Leaves	8.0 \pm 2.0	dirt	6.0 \pm 2.0	2.0 \pm 2.3	A B
Straw	7.5 \pm 4.0	grass	6.5 \pm 4.0	1.2 \pm 1.9	A B
Straw	11.2 \pm 2.4	dirt	2.8 \pm 2.4	7.0 \pm 1.5	B C
Grass	12.5 \pm 0.9	dirt	1.5 \pm 0.9	11.0 \pm 1.9	C
Grass (with predator cues)	6.5 \pm 2.5	dirt	7.5 \pm 2.5	1.1 \pm 2.2	A B

substrate: $\chi^2 = 1.48$, DF = 2, $p = 0.477$; cues: $\chi^2 = 0.032$, DF = 1, $p = 0.857$). As in the laboratory experiment, the choice scores differed across treatments (Table 2) with *Pardosa* exhibiting the strongest preference for grass over bare dirt when no predator information was available (Table 3). The prior occupancy of an enclosure by *Hogna* caused significant shifts in habitat selection by *Pardosa* in all three treatments (Table 2). For the treatments where a more complex substrate (grass or plant debris) was paired with bare dirt, *Pardosa* moved away from where we found the *Hogna* (Table 3); however, when grass was opposite plant debris, *Pardosa* moved into the plant debris even though we did not uncover a clear preference on the part of *Hogna* (Table 3).

Prey consumption

Laboratory experiment

Prior to experimentation, *Pardosa* assigned to treatments were similar in body size as evidenced by carapace width ($F = 0.261$, DF = 7, $p = 0.968$) and abdomen width ($F = 0.527$, DF = 7, $p = 0.813$, Table 4). Overall, the abdomen width increased over the 24 h of this laboratory experiment, which indicates that the spiders consumed prey, but some treatment differences emerged (Table 4, Fig. 1, $F = 2.96$, DF = 7, $p = 0.0062$). Both habitat and predator cues affected prey consumption (as evidenced by the change in

abdomen width) and there was a significant interaction between them (Table 2). There were no significant differences in this measure of prey consumption across the various habitat substrates tested when no predator information was present but when *Hogna* cues were in the aquarium, *Pardosa* consumption was lower in the grass and bare dirt habitats (Fig. 1).

Field experiment

There were no differences in the carapace width ($F = 0.749$, DF = 5, $p = 0.588$) or abdomen width ($F = 1.547$, DF = 5, $p = 0.175$) among the *Pardosa* assigned to the various treatments prior to experimentation (Table 4). Neither substrate nor predator cues affected survival of *Pardosa* in field enclosures (Cochran-Mantel-Haenszel test: substrate: $\chi^2 = 0.420$, DF = 2, $p = 0.810$; cues: $\chi^2 = 1.12$, DF = 1, $p = 0.123$). Abdomen width increased during the experiment, which verifies that the spiders consumed prey during the three days of this experiment and treatment differences emerged ($F = 8.182$, DF = 5, $p < 0.0001$, Table 4, Fig. 2). Both substrate and *Hogna* cues significantly affected prey consumption in field enclosures and the interaction was not significant (Table 2). Predator cues reduced consumption in all substrates (Fig. 2) and pairwise comparisons reveal that spiders consumed the most in grass habitat with no predator cues and the least when in plant debris with predator cues (Fig. 2).

Table 2. Summary results of the two-way ANOVAs of data from various experiments including the choice scores from the field habitat choice experiment, the change in abdomen width (our measure of prey consumption) for all the laboratory and field foraging experiments and the number of crickets killed in the prey capture experiment.

Factor	DF	SS	F	p-value
Field habitat choice experiment-choice scores				
Substrate	2	24403.6	42.23	0.1398
Cues	1	43604.2	150.93	0.0124
Substrate \times cues	2	8817.3	14.26	0.4322
Laboratory prey consumption experiment-abdomen width change				
Substrate	3	0.2	6.24	0.0008
Cues	1	0.2	18.52	<0.0001
Substrate \times cues	3	0.2	6.93	0.0004
Field prey consumption experiment – abdomen width change				
Substrate	2	106.9	3.48	0.0472
Cues	1	128.6	8.36	0.0080
Substrate \times cues	2	7.7	0.25	0.7798
Laboratory prey capture experiment – crickets killed				
Substrate	1	177.6	30.2	0.0001
Predator	2	254.0	21.6	0.0001
Substrate \times predator	1	0.72	0.06	0.9410
Laboratory prey capture experiment – abdomen width change				
Substrate	1	0.050	0.84	0.3613
Predator	1	0.013	0.22	0.6440
Substrate \times predator	1	0.001	0.01	0.9378

Table 3. The mean percent (\pm SE) of *Pardosa* observed in each habitat substrate and the choice scores for each pairing for the field habitat choice experiment. Choice scores indicated with different letters were significantly different using Tukey post-doc test ($p < 0.05$).

Substrate 1	Percent	Substrate 2	Percent	Choice score	
No cues present					
Grass	85.3 \pm 9.0	dirt	14.7 \pm 9.1	70.9 \pm 12.4	A
Grass	51.3 \pm 16.3	plant debris (leaves)	48.7 \pm 16.4	1.5 \pm 16.9	B
Plant debris	52.1 \pm 19.2	dirt	48.8 \pm 19.3	3.7 \pm 20.9	B
Cues deposited					
Grass	40.7 \pm 25.2	dirt	59.3 \pm 11.3	-17.0 \pm 11.9	B,C
Grass	33.4 \pm 6.0	plant debris	66.7 \pm 6.0	-31.9 \pm 11.6	C
Plant debris	32.1 \pm 9.7	dirt	67.9 \pm 9.8	-36.6 \pm 7.8	C

Prey capture of *Pardosa* and *Hogna*

Measurements of the carapace and abdomen reveal that there were some differences in the carapace width ($F = 2.23$, $DF = 3$, $p = 0.0914$) and abdomen width ($F = 5.46$, $DF = 3$, $p = 0.0019$) of the *Pardosa* assigned to various treatments. Specifically, the abdomen width of *Pardosa* was slightly smaller, according to Tukey tests, in the straw habitat with no *Hogna* than either of the treatments with *Hogna* present (Table 4). However, the overall body condition measured as the ratio of the abdomen to the carapace did not differ between treatments ($F = 1.83$, $DF = 3$, $p = 0.145$). Although abdomen size increased during treatments, there were no significant differences in the change in abdomen width across the predator or habitat treatments in this two hour experiment (Table 2). However, both substrate and spider treatments affected the number

of crickets killed across treatments (Table 2). The presence of straw reduced prey capture for both *Hogna* and *Pardosa* whether they were foraging alone or together (Fig. 3). When they were together, *Hogna* captured *Pardosa* more often on bare dirt than when the straw substrate was present (1 of 20 killed in straw; 9 of 20 in dirt) (Fisher exact probability test, $p = 0.0084$). When the two spider species were together, total cricket capture was similar to the capture of a single *Pardosa* (Fig. 3). When alone, the larger *Hogna* captured fewer crickets than *Pardosa* in both habitat types (Fig. 3).

Discussion

Clearly, predation risk has a powerful influence on *Pardosa* behavior, causing shifts in habitat use and

Table 4. Measurements (mean \pm SD) of the carapace width and abdomen width taken of *Pardosa* before and after foraging in prey consumption and prey capture experiments. The carapace width is fixed at adulthood and is a measure of total size. The difference between abdomen width measurements made before and after foraging provide evidence of ingestion.

Experiment	Treatment	N before	Carapace (mm)	Abdomen before (mm)	N after	Abdomen after (mm)
Prey consumption-laboratory						
	straw	20	2.23 \pm 0.19	2.17 \pm 0.19	20	2.48 \pm 0.25
	leaves	20	2.25 \pm 0.13	2.13 \pm 0.27	20	2.33 \pm 0.23
	grass	20	2.27 \pm 0.25	2.19 \pm 0.11	20	2.40 \pm 0.25
	dirt	20	2.23 \pm 0.26	2.10 \pm 0.18	20	2.53 \pm 0.28
	straw with cues	20	2.27 \pm 0.16	2.09 \pm 0.28	20	2.27 \pm 0.25
	leaves with cues	20	2.30 \pm 0.18	2.16 \pm 0.26	20	2.39 \pm 0.33
	grass with cues	20	2.26 \pm 0.20	2.16 \pm 0.21	20	2.23 \pm 0.19
	dirt with cues	20	2.26 \pm 0.16	2.19 \pm 0.26	20	2.39 \pm 0.28
Prey consumption-field						
	debris	50	2.22 \pm 0.21	2.10 \pm 0.23	50	2.39 \pm 0.32
	grass	50	2.20 \pm 0.22	2.04 \pm 0.21	49	2.55 \pm 0.40
	dirt	50	2.20 \pm 0.21	1.98 \pm 0.26	48	2.43 \pm 0.39
	debris with cues	50	2.19 \pm 0.22	2.08 \pm 0.31	50	2.22 \pm 0.38
	grass with cues	50	2.14 \pm 0.22	2.00 \pm 0.37	49	2.17 \pm 0.39
	dirt with cues	50	2.19 \pm 0.15	2.10 \pm 0.29	47	2.23 \pm 0.32
Prey capture-laboratory						
	dirt	20	2.18 \pm 0.16	1.95 \pm 0.24	20	2.45 \pm 0.25
	straw	20	2.10 \pm 0.18	1.83 \pm 0.22	20	2.23 \pm 0.27
	dirt with <i>Hogna</i>	20	2.17 \pm 0.18	2.02 \pm 0.19	11	2.45 \pm 0.25
	straw with <i>Hogna</i>	20	2.16 \pm 0.16	2.10 \pm 0.24	19	2.47 \pm 0.26

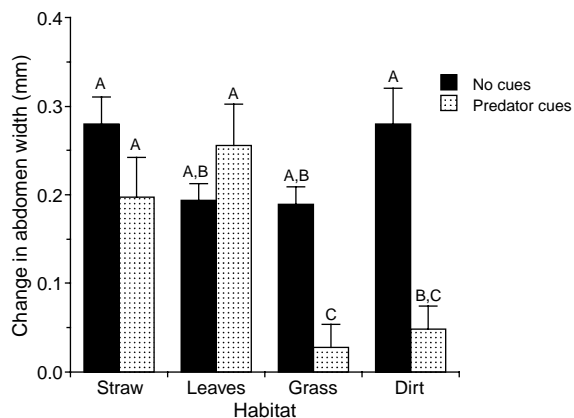


Fig. 1. The change in abdomen width (mean \pm SE), our measure of prey consumption, for *Pardosa* that fed on crickets in four different habitat substrates in the laboratory. Closed bars represent the change with uncontaminated substrates and open bars represent the change with predator cues. Bars indicated with different letters are significantly different by Tukey post-hoc test ($p < 0.05$).

depressing prey consumption. Specifically, in both laboratory and field, *Pardosa* showed a distinct preference for grass over bare dirt; a preference that was eliminated when predator cues were present (Table 1, 3). Interestingly, in field trials where *Hogna* was allowed to deposit cues in either or both substrates, they caused *Pardosa* to be more selective than they were in treatments with no *Hogna* information (Table 3). Additionally, *Pardosa* prey consumption was depressed by predator cues and that effect was most dramatic in laboratory trials with the grass and bare dirt, which were

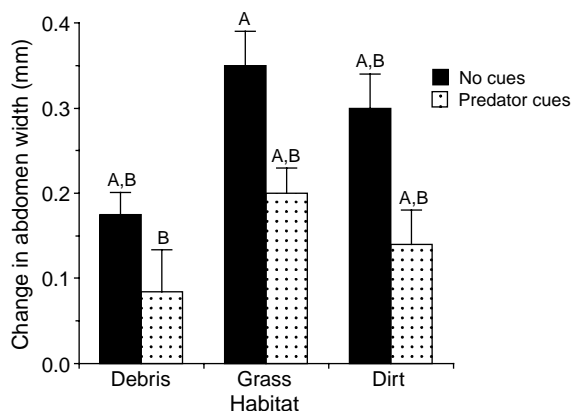


Fig. 2. The change in abdomen width (mean \pm SE), our measure of prey consumption, for *Pardosa* foraging in field enclosures with three different habitat substrates. Closed bars represent the changes with uncontaminated substrates and open bars represent the changes with predator cues. Bars indicated with different letters are significantly different by Tukey post-hoc test ($p < 0.05$).

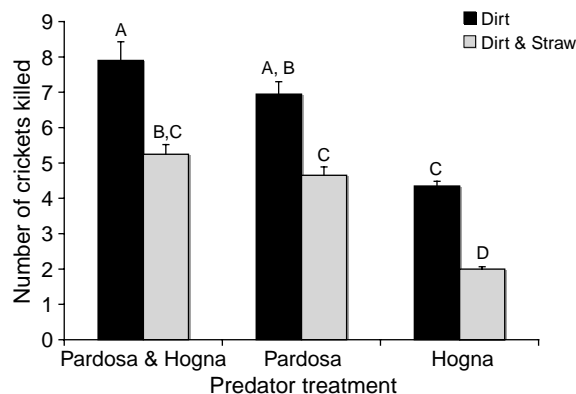


Fig. 3. The number of crickets captured (mean \pm SE) by *Pardosa* and/or *Hogna* in laboratory containers. Closed bars indicate predators foraging in containers with bare dirt and open bars those where straw was added. Bars indicated with different letters are significantly different by Tukey post-hoc test ($p < 0.05$).

the two substrates that *Pardosa* discriminated between most definitively in both laboratory and field experiments (Fig. 1, 2). The final experiment revealed that *Pardosa* captured and killed more crickets but were nine times more likely to fall prey to *Hogna* on bare dirt than when straw was added to small laboratory enclosures (Fig. 3). Taken together, these results confirm that *Pardosa* were confronted with a tradeoff between habitat quality and predation risk that affected habitat selection, distribution and foraging success.

Shifts in space use by *Pardosa* in the presence of silk and excreta from *Hogna* have been observed in laboratory cups (Persons et al. 2002, Folz et al. 2006) but never before tested with substrates approximating those they might encounter in a natural situation. In the laboratory, we confined *Hogna* to the preferred grass habitat so the choice was really one of selecting between areas with or without predator cues, however, in field enclosures, *Hogna* were free to roam throughout both habitat options prior to the introduction of *Pardosa*. That prior occupancy by *Hogna* affected *Pardosa*'s habitat selection in all habitat combinations suggests that, all else being equal, both species select similar habitat features.

The fact that *Pardosa* readily shifted habitat preferences when predators were detected and foraged equally well across a variety of substrates when predator cues were not present (Fig. 1, 3) suggests that *Pardosa* are generalists that make broad use of a heterogeneous landscape (Marshall and Rypstra 1999, Marshall et al. 2000, 2002, 2006). This versatility may make it possible for *Pardosa* to move away from *Hogna* when necessary and still find food and function successfully. On the other hand, Finke and Denno (2002) found that structurally complex substrates reduced intraguild

predation by another *Pardosa* species (*Pardosa littoralis*), which lead to a stronger impact of the predatory arthropod community in the food web. Although *Pardosa* were more likely to survive *Hogna* predation in laboratory containers with straw added for complexity, there was no effect on the total number of crickets killed when both spider species were present (Fig. 3). However, this short-term (2 h) laboratory experiment was simply aimed to explore the relative effects of habitat and predation risk on prey capture. Further experimentation is required to determine how these responses compare to the results of Finke and Denno (2002) in the manner in which they play out in the food web.

Given the specificity of the reactions of *Pardosa* to *Hogna* cues in other studies (Persons et al. 2001, Lehmann et al. 2004, Bell et al. 2006), the fact that *Pardosa* seemed able to ignore predator information in straw and leaf habitats and continue to consume prey to the same degree (Fig. 1) suggests that they perceived those habitats as less risky. As mentioned, the ability of *Hogna* to capture *Pardosa* or crickets was impaired in the complex straw substrate (Fig. 3) and this reduction may, in fact, be sufficient to embolden *Pardosa* to discount predator information in the presence of certain habitat features. Alternatively, if the substrate has a direct or indirect effect on the amount, distribution and efficacy of the cues that *Pardosa* uses to detect *Hogna*, then that could account for the differential in *Pardosa*'s response across substrates. It seems unlikely that *Hogna* would somehow be better able to hide its chemical signature in some habitats and not others, especially since prior occupation by *Hogna* was sufficient to reduce prey consumption across the board and shifted all previous habitat use patterns in field enclosures (Fig. 2, Table 3). On the other hand, a number of insect species, including crickets, recognize and alter their behavior in the presence of spider chemical cues (Snyder and Wise 2000, Williams et al. 2001, Hlivko and Rypstra 2003, Kortet and Hedrick 2004). Therefore, it is possible that the combined behavioral responses of *Pardosa* and crickets to *Hogna* cues lead to the differences in the *Pardosa* prey consumption in the straw and leaf substrates. The fact that we saw no similar differences in prey consumption among substrates in the field studies may be due to the fact that a wider diversity of arthropod prey were available to *Pardosa* since the enclosures were open at the top and could easily be invaded by any number of flying insects.

Although previous studies have revealed that substrate complexity influences *Pardosa* density (Marshall and Rypstra 1999, Marshall et al. 2000, Finke and Denno 2002), we observed no strong preferences for more heterogeneous substrates except when grass was paired with bare dirt. *Pardosa* is an active forager with an excellent ability to colonize new habitat patches and

populations are relatively insensitive to the presence of habitat edges or the degree of fragmentation (Walker et al. 1999, Marshall et al. 2000, 2006). A congener that occupies the agricultural fields of Europe has been shown to make broad use of the soil surface features and range up to 70 m over several weeks (Samu et al. 2003). Thus the lack of strong preferences among the substrates tested here may be an indication that this species has a broader view of the soil surface landscape than we captured in our laboratory aquaria or field enclosures. Where we were looking for discrete preferences between paired habitats in confinement, the spiders may have been viewing the entire arena as a subset of a single patchy habitat not unlike the agroecosystems where they are common (Marshall and Rypstra 1999, Marshall et al. 2002).

The habitat choice and prey consumption trials presented here all included more than one animal. We designed the experiments this way because *Pardosa* normally occurs at high densities in agroecosystems ranging from 5 to 90 m² (Marshall and Rypstra 1999, Marshall et al. 2000, 2002, 2006) and cannibalism among similarly sized females is rare (Balfour et al. 2003, Rypstra and Samu 2005). We reasoned that only by including multiple animals in experimental arenas could we understand habitat choice and foraging success in the face of their common natural conspecific interactions. Even though interference among conspecifics may have affected our measures of habitat selection and/or prey consumption, it would not be likely to change our findings. Conspecific interactions or territoriality would cause some animals to move into less desirable habitat in the habitat choice experiments and reduce their foraging effectiveness in the prey consumption experiments and thus reduce our ability to detect differences across treatments. Thus, we are confident that the differences we uncovered are realistic responses to the habitats we tested, much more representative of what the spiders experience in a natural situation than if we had run experiments with isolated individuals.

This study suggests that the "landscape of fear" concept can enhance our understanding of arthropod habitat selection, distribution and foraging. Ultimately this conceptual approach may be useful as we try to uncover more of the complex interactions among arthropods in the food web and how they affect biological control. Specifically, *Pardosa* individuals fed successfully in all substrates, moved easily to alternative habitats when threatened and reduced foraging activity when no alternative habitat was available. Thus, there are two ways that fear among predators can affect the community and each one would have an opposite effect in the food web. If the dominant effect of risk were to reduce foraging where predators overlap, then the net effect would be to reduce top down effects thereby

increasing herbivory and reducing plant production. Alternatively, if risk primarily causes shifts in habitat use then it would reduce intraguild predation and lead to a more even distribution of heterospecific predators across the landscape. This scenario would result in higher predator populations and more effective predatory coverage of an area leading to lower herbivore populations and greater plant production. Further study is needed to understand the scale at which these predators respond to one another and to different habitat features in order to integrate the physical landscape and the landscape of fear into our understanding of the food web in agroecosystems.

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