

Effects of Predation Risk on Vertical Habitat Use and Foraging of *Pardosa milvina*

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Abstract

Animals face the risk of predation while engaging in regular activities, such as foraging, mate-seeking, and reproducing. In order to avoid predation, prey can modify behavior to prevent capture. *Pardosa milvina* may climb in response to chemotactile cues of *Hogna helluo*, a larger cooccurring wolf spider, to avoid predation. The purpose of this study was to test the effects of the location of predator cues on the climbing response of *P. milvina* and to test how this antipredator behavior affected foraging success. In experimental arenas, when cues were on the bottom of the containers, *P. milvina* moved upward, and when cues were on the walls, individuals moved downward. These results suggest that *P. milvina* respond to *H. helluo* cues with general avoidance and do not automatically climb in response to the cues. As *H. helluo* spend most of their time on the ground, *P. milvina* may avoid predation by spending more time climbing in areas with *H. helluo* cues. The presence of predator cues significantly decreased foraging by *P. milvina*. But within the predator cue treatments, climbing ability had no effect on foraging, possibly due to the short height of the feeding arenas. Future studies are needed to determine if climbing by *P. milvina* in response to cues of *H. helluo* has direct and indirect negative effects on herbivores in the field.

Introduction

Predation can act as a strong selection pressure favoring adaptations in prey to avoid being killed (Lima 1998; Lima & Dill 1990; Cloudsley-Thompson 1995; Lass & Spaak 2003). Prey may use a variety of sensory modalities to detect the presence of a predator, including visual, seismic, auditory, and chemical (Lima & Dill 1990). Of these, chemical cues may be particularly useful because they allow prey to assess predation risk without coming into visual contact with the predator and can provide detailed information about predator size, diet and the amount of time since the predator was in the area (Snyder & Wise 2000; Dicke & Grostal 2001; Persons et al. 2001). Recent evidence suggests that chemical cues

may be used by a variety of species in predator detection, including some species that were once thought to rely primarily on visual cues (Kats & Dill 1998; Dicke & Grostal 2001).

Once a predator has been detected by chemical cues, prey can modify their behavior to avoid capture. Predator avoidance behavior in response to chemical cues has been studied in many species and often involves decreased activity and use of refugia (reviewed in Lima & Dill 1990; Kats & Dill 1998). Most of these studies, however, have been conducted in aquatic ecosystems (Kats & Dill 1998; Lass & Spaak 2003). For example, a great deal of information has documented that zooplankton respond to fish-exuded kairomones with increased diel vertical migration, a daily cycle of changes in water depth

(reviewed in Hays 2003). By spending the day in deeper and darker waters and the night at surface waters, zooplankton are able to avoid high risks of predation from visually hunting predators and also feed on abundant food sources in the surface waters (Zaret & Suffern 1976; Hays 2003). Hence, vertical movements by prey may be an effective predator avoidance behavior that balances the risk of predation and foraging needs.

While vertical movements have been most frequently studied in aquatic ecosystems, they may also aid in predator avoidance in terrestrial systems. In south-western Ohio, the wolf spiders *Hogna helluo* (300–800 mg) and *Pardosa milvina* (20–30 mg) are frequently found at relatively high densities in agricultural fields (Marshall et al. 2000, 2002). The larger *H. helluo* readily preys upon the smaller *P. milvina* if given the chance (Persons et al. 2001). However, *P. milvina* are very sensitive to chemotactile cues (silk and excreta) from *H. helluo* and can modify their behavior in response to the size, diet and hunger level of the predator in ways that significantly enhance survival (Persons & Rypstra 2001; Persons et al. 2001; Barnes et al. 2002, Bell et al. in press). In particular, Persons et al. (2002) observed that *P. milvina* climbed upon the sides of their laboratory containers when the chemotactile cues of *H. helluo* covered the bottom. Climbing vegetation may decrease the risk of predation for *P. milvina* because, while both spiders are ground dwelling, *H. helluo* may be particularly associated with the substrate because juveniles and females often build burrows (Walker et al. 1999; Persons et al. 2002).

The purpose of this study was to explore vertical movement as an antipredator behavior of *P. milvina* in response to chemotactile cues (hereafter referred to as cues) from *H. helluo* and to examine if this vertical behavior has a foraging cost. We first examined the vertical habitat use of *H. helluo* to determine if they preferred to remain on the ground surface, as we had predicted. We then tested if the location of *H. helluo* cues affected the vertical movement of *P. milvina* by placing predator cues on the bottom or sides of containers. If *H. helluo* spend most of their time on the soil surface, then there may be a selection for *P. milvina* to increase climbing automatically whenever predator cues are encountered. Alternatively, climbing may simply be an attempt to move away from cues, in which case we would expect upward movements when cues are on the substrate and downward movements when cues are on the side of containers. Finally, we tested if climbing in the presence of cues affected foraging success by

manipulating the ability of *P. milvina* and their prey to climb in experimental arenas. Previous studies indicate that the presence of *H. helluo* cues reduces foraging by *P. milvina* (Persons et al. 2002). We predicted that if *P. milvina* are allowed to climb but their prey are not, then there will be an additional reduction in foraging (above the general reduction in foraging in the presence of predator cues) due to the spatial separation of *P. milvina* and their prey.

Methods

General Protocol

Pardosa milvina were collected from the soybean fields at Miami University's Ecology Research Center (ERC; Oxford, Butler County, OH, USA). *Hogna helluo* used in this study were the first-generation, laboratory-reared offspring of individuals that were collected at the ERC. All spiders were housed in individual plastic containers (*P. milvina*: diameter = 5.5 cm × height = 5.5 cm; *H. helluo*: diameter = 12 cm × height = 9 cm) with 2 cm of damp peat moss covering the bottom of the cup to prevent desiccation. Cups were housed in an environmental chamber at 25°C and 70% relative humidity on a 13L:11D photoperiod. When not being used in experiments, *P. milvina* were maintained on a diet of two pinhead crickets (2 mm; *Acheta domesticus*) two times per week and *H. helluo* were maintained on a diet of one 4-wk-old cricket one time per week.

Expt I: Predator Habitat Use

In this experiment, we examined vertical habitat use of the predator, *H. helluo*. Trial arenas consisted of a 1.4-l Rubbermaid® container (Rubbermaid®, Fairlawn, OH, USA) (12-cm diameter × 12-cm height) swabbed with 70% ethanol prior to use. The arenas were completely lined with Mead Sketch Pad Paper cut into two pieces. A circular piece (13.5 cm in diameter) was carefully taped to the bottom of the container using double-sided tape. A rectangular piece (10.5 cm × 42 cm) lined with 10 pencil lines 1 cm apart along the long axis of the paper was carefully taped onto the inside of the container using double-sided tape. These lines allowed us to measure the vertical location of *H. helluo* during trials. *Hogna helluo* (n = 18) were randomly selected and moved to an environmental chamber on a 12L:12D photoperiod for 3 wks prior to experimentation. During this orientation period, no change was made to the spiders' diets. One day prior to experimentation,

H. helluo were fed one 1/4-inch cricket each. On the day of the experiment, the spiders were placed into prepared arenas. We recorded the vertical position as the vertical location of the chelicerae of *H. helluo* in the arenas once every 20 min for 8 h (for 4 h each during the light and dark part of the light cycle). During the dark period, a portable red light was used to observe the location of *H. helluo*. We used a repeated-measures analysis of variance (ANOVA) with time as the only effect to test if the vertical location of *H. helluo* varied over the course of the observation period.

Expt II: Climbing on Cues

In this experiment, we examine the effects of *H. helluo* cue location on the vertical location of *P. milvina*. Experimental arenas were lined with paper in the same manner as expt I. Arenas were prepared according to four treatment types ($n = 14$ per treatment): no cues, cues on the bottom only, cues on the side only, and natural cue placement (i.e. cue location determined by *H. helluo*). Cue collection was done in separate containers. Cues on the circular paper were collected in additional arenas where the circular piece of paper covered the bottom of the container and cues on the rectangular paper were collected in rectangular arenas (42-cm length \times 12-cm width) in which the paper covered the entire bottom of the container. Twenty-four hours prior to silk and excreta collection, all *H. helluo* were fed to satiation with approximately six 1/4-inch crickets. Just prior to experimentation, the experimental arenas were swabbed with 70% ethanol and the cue-laden or blank paper was taped along the sides and bottom of the arena.

Arenas prepared for the no cues treatment contained untreated paper. For the cues on the bottom only treatment, a satiated *H. helluo* was allowed to walk along a circular bottom piece of paper for 24 h prior to experimentation. This circular piece of paper was then placed in the arena with an untreated rectangular piece covering the sides. For the cues on the side only treatment, a satiated *H. helluo* was allowed to walk along a pencil-lined rectangular piece of paper for 24 h prior to experimentation. An untreated circular paper was taped into the bottom of the arena and the cue-laden rectangular piece was taped to the sides. For the natural cue placement treatment, a satiated *H. helluo* was allowed to occupy the experimental arena for the 24 h preceding the trial. During this time, the *H. helluo* was free to move about the arena and place cues (e.g. silk draglines and excreta). All *H. helluo* used for cue

collection were removed just prior to the placement of their cue-laden paper in the experimental arenas.

All trials were conducted in an isolated room to reduce the chance of disturbance. *Pardosa milvina* were introduced into the experimental arenas and given 10 min to acclimate before data collection began. During trials, the arenas were covered with square sections of Plexiglass to prevent spider escape. We recorded the vertical location of the chelicerae of each spider to 0.5 cm using the lines on the paper as a guide. Scan samples were taken every 10 min for an hour ($n = 6$ measurements per spider). We calculated the change in vertical location of *P. milvina* by subtracting the vertical location at the first time period from the vertical location at the last time period. Average vertical location across all six time periods, vertical location at the beginning of the trial, vertical location at the end of the trial and change in vertical location were compared among treatments using a one-factor ANOVA.

Expt III: Foraging and Climbing

In this experiment, we examined the effects of chemical cues and ability to climb on foraging by *P. milvina*. Trial arenas consisted of opaque plastic cups (diameter = 12 cm \times height = 9 cm) with a peat moss substrate. The substrate was prepared by homogenizing a dilute mixture of water and peat moss in a blender. This mixture was then poured into the cups to a depth of 2 cm and allowed to dry so that a smooth surface was available during the trial. After drying, any debris on the sides of the arena was wiped clean. *Pardosa milvina* were never observed climbing the cleaned walls of these cups. Arenas were prepared according to four treatment types: (1) no cues, no climbing, (2) cues, no climbing, (3) cues, climbing for *P. milvina* only and (4) cues and climbing for both *P. milvina* and pinhead crickets.

Arenas of the no cues treatment consisted of unmanipulated cups. For the other three treatments, predator cues were collected by allowing a satiated *H. helluo* to occupy the container and deposit cues for 24 h prior to experimentation, after which time it was removed from the containers. Arenas for the cues, no climbing treatment contained predator cues and had cleaned walls. Arenas for the cues, climbing for *P. milvina* only treatment contained predator cues and three strips of paper (3.5 cm \times 4.5 cm) that were taped onto the side of the arena with the bottom edge approximately 0.75 cm above the surface of the arena. This height of the paper ensured that

P. milvina were able to reach and climb on the paper while the pinhead crickets could not. Arenas for the cues, climbing for both *P. milvina* and pinhead crickets treatment contained cues and strips of paper similar to those used in treatment 3 except that the paper touched the bottom surface of the arena in this treatment. Both *P. milvina* and the pinhead crickets were able to reach and climb on the paper at this height.

Prior to the trials, *P. milvina* were fed two 10-d-old crickets and then starved for 4 d to standardize hunger, which can affect the response to predator cues (Walker & Rypstra 2003). At the start of the trials, a *P. milvina* was introduced into an experimental arena with eight pinhead crickets and allowed for forage to 90 min. We compared the number of crickets consumed among treatments using a one-factor ANOVA.

Results

Expt I: Predator Habitat Use

While 17% (three of 18) of *H. helluo* were observed at the top of the arena during at least one time period, 61% (11 of 18) of individuals remained on the bottom of the containers for the entire trial (Fig. 1). Only 33% of individuals climbed higher than 4 cm and no *H. helluo* were observed climbing in more than 33% (eight of 24) of the observation periods. There was a significant effect of time on climbing by *H. helluo*, which was due to small amounts of climbing just after the onset of darkness ($F_{1,413} = 3.93$, $p = 0.048$).

Expt II: Climbing on Cues

Pardosa milvina were frequently observed climbing and were able to climb the full extent of the experimental arenas. The average vertical location

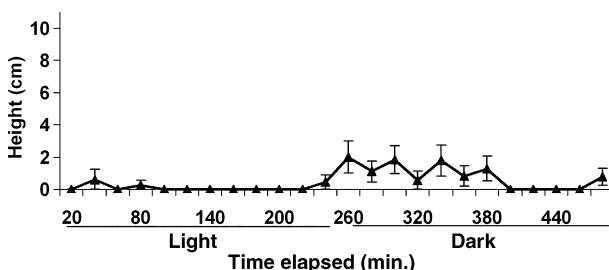


Fig. 1: The \bar{x} (± 1 SE) vertical location of *Hogna helluo* in experimental arenas during 4 h of light and 4 h of dark

of individuals (i.e. the average for each individual among the six time periods) did not differ among the cue placement treatments ($F_{3,52} = 0.76$, $p = 0.52$). This may have been because it took time for *P. milvina* to respond to the predator cues. At the beginning of the trials, there was no effect of cue treatment on *P. milvina* vertical location ($F_{3,52} = 2.20$, $p = 0.10$). However, by the end of the experiment, there were significant differences in vertical location (Fig. 2; $F_{3,52} = 3.07$, $p = 0.04$). Individuals in the bottom cue treatment were located at the highest vertical location, individuals in the side cue treatment were located at the lowest vertical location and individuals in the blank and natural cue treatments were located at intermediate vertical locations (Fig. 2). There were also significant differences among treatments in the change in vertical location (i.e. final vertical location – initial vertical location) during the course of the trials (Fig. 2; $F_{3,52} = 4.41$, $p = 0.008$). The change in vertical location for spiders in the bottom and natural cue placement treatments was significantly higher than that for individuals in the side cue and control treatments (Fig. 3).

Expt III: Foraging and Climbing

The presence of *H. helluo* cues resulted in a significant reduction in the number of crickets consumed by *P. milvina* (Fig. 4; $F_{3,52} = 4.13$, $p = 0.01$). However, climbing had no additional effect on foraging as the number of crickets consumed was not significantly different among the cues with no climbing, cues with *P. milvina* climbing only and cues with *P. milvina* and cricket climbing treatments (Fig. 4).

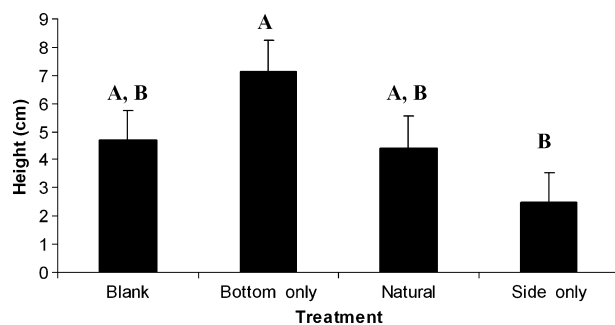


Fig. 2: The \bar{x} (± 1 SE) final vertical location of *Pardosa milvina* among treatments with varying placements of predator cues. Treatments with different letters are significantly different ($p < 0.05$) as determined by Tukey's post hoc tests

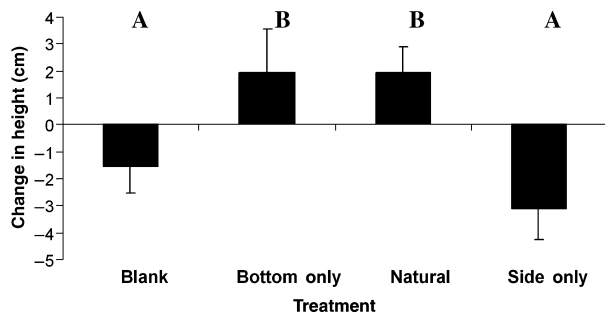


Fig. 3: The \bar{x} (± 1 SE) change in vertical location (i.e. vertical location at 60 min – vertical location at 10 min) for *Pardosa milvina* in arenas with cues in different locations. Treatments with different letters are significantly different ($p < 0.05$) as determined by Tukey's post hoc tests

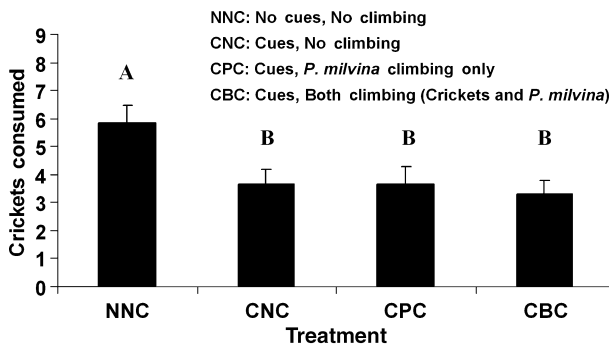


Fig. 4: The \bar{x} (± 1 SE) number of pinhead crickets consumed by *Pardosa milvina* in arenas with and without cues and with and without a climbing surface. Treatments with different letters are significantly different ($p < 0.05$) as determined by Tukey's post hoc tests

Discussion

Pardosa milvina displayed flexible climbing behavior in response to the location of predator cues. When cues were on the bottom of the arena, *P. milvina* climbed upward and were located at higher vertical locations in the containers. When cues were on the sides of the arena, *P. milvina* climbed downward and were located on the ground or lower in the container. This behavior is consistent with the hypothesis that climbing by *P. milvina* in the presence of predator cues is an attempt to avoid cue-laden substrates and not a general response whenever cues are encountered.

Pardosa milvina may benefit from flexible climbing behavior because *H. helluo* display periodic climbing. While *H. helluo* remain on the ground most of the time, *H. helluo* were periodically observed climbing in our laboratory experiment and individuals are sometimes captured 0.5 m high or more in vegetation in

the field (S. M. Wilder, personal observation). Climbing behavior of *P. milvina* did not appear to incur a significant foraging cost. While *P. milvina* displayed a strong and consistent reduction in foraging in the presence of predator cues, there was no effect of climbing ability of either *P. milvina* or both *P. milvina* and their prey on foraging. The balance of costs and benefits of flexible climbing behavior for *P. milvina* may explain why climbing is not a fixed strategy.

The response of *P. milvina* to the cues of *H. helluo* was not immediate. After 10 min, there were no differences in location among the treatments. However, over the course of the experiment, *P. milvina* adjusted their vertical location so that by the end of the experiment the spiders in the treatment with cues on the bottom were high in the arenas and the spiders in the treatment with cues on the sides were low in the arenas. The delay in the response to cues from *H. helluo* may be because of the fact that these cues cause a reduction in the time spent moving and speed of *P. milvina* (Persons & Rypstra 2001; Persons et al. 2001, 2002; Barnes et al. 2002). Reduced movement by *P. milvina* decreases their visibility to *H. helluo*, which detect prey using visual and vibratory cues, and results in a lower risk of predation (Persons et al. 2001, 2002). Hence, while it may be beneficial for *P. milvina* to move higher in the vegetation when they detect predator cues on the ground, they must make this movement slowly so as to not attract the attention of *H. helluo*.

In our experiment, there was no effect of climbing ability on the foraging success of *P. milvina*. In the presence of cues, we predicted that if *P. milvina* were able to climb but the crickets were not, then there would be a reduction in foraging because *P. milvina* and their prey would be spatially separated. However, the experimental arenas that we used for the foraging experiment were only 4.5 cm high. At this low height, *P. milvina* can detect movement by prey. Thus, in the treatment where only *P. milvina* were able to climb, we may not have observed a further decrease in foraging (i.e. in addition to the effect of cues) because *P. milvina* may have made brief forays to the soil surface to capture prey when the prey were observed moving. This suggests that when prey are located on the substrate, vertical location may be an important factor affecting the consequences of climbing for foraging.

Under field conditions, the effects of climbing on foraging by *P. milvina* may also depend on the vertical distribution of prey. Very little information is available on the quantity of prey items available to *P. milvina* on the soil surface relative to plants. How-

ever, the encounter rate with prey may be lower while climbing. For example, while *P. milvina* can encounter prey in any direction while on the soil surface, they can only encounter prey in two directions, up and down the plant stem, while climbing. In addition, larger prey may be difficult or risky to capture while climbing on vertical surfaces. Wolf spiders sometimes grasp large prey using all eight legs until the venom is able to fully immobilize the prey (Foelix 1996). But, while on vertical surfaces, *P. milvina* must keep some legs on the surface or they will fall to the ground. Constraints on the number of legs available to subdue prey, due to climbing, may expose *P. milvina* to the risk of damage from retaliation by prey and restrict the size of prey that can be captured. Lower encounter rates with prey and a smaller size range of available prey may result in reduced foraging by *P. milvina* when climbing in nature.

Intraguild predation can have negative effects on biological control of crop pests by predators (Polis et al. 1989; Rosenheim et al. 1995; Hodge 1999; Snyder & Ives 2001). However, in our system, intraguild predation by the larger *H. helluo* may have selected for antipredator behavior (i.e. climbing) in *P. milvina* that could have a positive impact on biological control of crop pests. *Pardosa milvina* and *H. helluo* can reach relatively high densities in agricultural fields (Marshall et al. 2000). If only one of these wolf spiders inhabited an area, then that species, regardless of which one it was, would likely remain on the soil surface. However, when they are syntopic, the presence of *H. helluo* may force some *P. milvina* to occupy and forage in the vegetation. While foraging on the vegetation, *P. milvina* may be able to reduce plant damage by consuming herbivorous insects. In addition to the direct effect of consuming herbivores, *P. milvina* may have indirect effects on herbivory because the silk draglines they leave as they move through the vegetation reduce the foraging of herbivorous insects (Hlivko & Rypstra 2003). Further research is needed to examine if this effect results in a significant reduction in plant damage in nature and if interactions among other intraguild predators can have similar effects.

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