

## RESEARCH PAPERS

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### **Preference for Chemical Cues Associated with Recent Prey in the Wolf Spider *Hogna helluo* (Araneae: Lycosidae)**

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#### **Abstract**

In the wolf spider, *Hogna helluo*, we tested the response to insect and spider prey chemical cues and whether they show a preference for cues associated with prey consumed most recently. Thirty adult female *H. helluo* were maintained on a diet of either females of a smaller co-occurring wolf spider (*Pardosa milvina*) or domestic crickets (*Acheta domesticus*). A single *P. milvina* or cricket nymph was maintained on filter paper for 24 h, after which the papers from both prey sources were simultaneously presented to individual *H. helluo* from each diet treatment group. *H. helluo* locomotor behavior on each treatment and initial substrate preference was recorded ( $n = 15/\text{treatment}$ ). *H. helluo* fed crickets showed significantly longer residence time and decreased mobility on filter paper previously occupied by a cricket; spiders fed *P. milvina* showed longer residence times and decreased mobility on filter paper previously occupied by *P. milvina*. *H. helluo* fed *P. milvina* exhibited an initial preference for substrates previously occupied by *P. milvina* but *H. helluo* fed crickets did not show a corresponding initial preference for crickets. Results suggest that *H. helluo* can detect distant cues associated with *P. milvina* but not crickets before contacting the substrate and that *H. helluo* respond to chemical cues from prey and show a preference for those cues associated with their most recent prey.

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#### **Introduction**

Animals may increase foraging efficiency through reduced search time by associating feces, volatile odors, or other indirect cues with particular prey. Associ-

ative learning of chemical cues with different prey types has been empirically demonstrated in many generalized arthropod predators (van Lenteren & Bakker 1975; Turlings et al. 1989; Papaj & Vet 1990; reviewed in Vet & Groenewold 1990; Godfray 1994) and in vertebrates (Nams 1991; Burghardt 1992). Some taxa, such as hymenopteran parasitoids and reptiles, have been studied extensively while others have received little attention. Despite considerable evidence that spiders are capable of detecting chemical cues in the form of sex pheromones from conspecifics (Schulz & Toft 1993; Watson 1986; Suter & Renkes 1982), there is little information regarding how, or if spiders respond to chemical cues produced from prey (Punzo & Kukoyi 1997; Persons & Uetz 1996a). Even fewer studies have examined spider learning and prey selection (Jackson & Wilcox 1993). Feces from prey, airborne chemical cues from pheromones or other odors, as well as silk draglines produced by other spiders may all be used as sources of information about prey location.

Wolf spiders (Lycosidae) are polyphagous predators and are generally believed to exhibit little prey preference (Nentwig 1986). Presumably, this is because wolf spiders are often food limited (Wise 1993) and may suffer from nutritional deficiencies if maintained on a monotypic diet (Greenstone 1979; Uetz et al. 1992). However, even if wolf spiders do not show obvious prey preference, prior feeding experiences may still bias prey searching and foraging behavior. Punzo & Kukoyi (1997) showed that the field-collected wolf spider, *Trochosa parthenus*, remained in patches for longer periods of time in the presence of chemical cues from prey found in its natural habitat relative to unfamiliar prey types. The wolf spider, *Schizocosa ocreata*, spent longer periods of time on substrates previously occupied by crickets than blank controls after they had been maintained on a diet of crickets (Persons & Uetz 1996a). Neither of these studies explicitly addressed whether the apparent preferences for particular prey cues were the result of prior feeding experience with those prey types. In this study, we tested the hypothesis that wolf spiders detect and alter their behavior in the presence of chemical cues associated with their most recently consumed prey.

#### Study Species and Prey

*Hogna helluo* (Walckenaer) is a large ground-dwelling wolf spider common to moist fields, forests, and marsh edges (Dondale & Redner 1990). It is also prevalent within and along margins of agro-ecosystems (Marshall & Rypstra 1999). *Pardosa milvina* Hentz is a smaller syntopic species of wolf spider and a common prey item of adult *H. helluo* (see Marshall & Rypstra 1999). We compared the behavior of *H. helluo* in response to cues from different prey. Specifically, we tested the hypothesis that adult female *H. helluo* will exhibit a preference for chemical cues associated with adult female *P. milvina* when maintained on a *P. milvina* diet and *H. helluo* maintained on a diet of crickets (*Acheta domesticus*) will show a preference for cricket chemical cues. These two prey types may have qualitatively and quantitatively different chemical cues. Both prey may produce feces as well as volatile compounds. However, *P. milvina*, like most cursorial spiders, also produce a silk dragline as they move through the environment which could be used by *H. helluo*

to locate them. For consistency, we chose to use cues from adult female *P. milvina* rather than adult males to control for any pheromones that may have been deposited on the filter paper with the silk and feces. Female *P. milvina* body mass is approximately twice that of males (M. H. Persons, unpubl. data) and the amount of silk and feces deposited could also be different between the sexes.

## Methods

### Collection and Maintenance

We collected subadult and mature female *H. helluo* from within and along the margins of soybean fields (Butler County, Ecology Research Center, Miami University, Oxford, OH, USA) in Jun. 1997 and used laboratory-reared offspring of these females for all experiments. Spiders were maintained on *Drosophila melanogaster* during early instars and cricket nymphs (*A. domesticus*) thereafter until maturity and were therefore naive about any other prey. Thirty females were maintained in opaque round plastic containers (9 cm high × 12 cm diameter) with 2–3 cm of a moistened peat moss substratum. Spiders were watered ad libitum and randomly assigned to a diet of either two medium-sized domestic crickets (*A. domesticus*) ( $\approx 1$  cm long) ( $n = 15$ ) or four adult male or female *P. milvina* wolf spiders ( $n = 15$ ) twice per week for at least 1 mo prior to testing. Spiders of both treatment groups were fed to satiation and then held without food for 9 d prior to testing to maintain similar hunger levels for both treatment groups. *H. helluo* fed *P. milvina* were given only adult females for the final two feedings prior to testing. All spiders were maintained at room temperature (23–25°C) on a 13 h light/11 h dark photoperiod.

### Stimulus Preparation

Chemical cues from *P. milvina* and crickets were collected on 20-cm half-circle sheets of filter paper. Either a single 1-cm long domestic cricket nymph (*A. domesticus*) or an adult female *P. milvina* were allowed to move on a filter paper sheet (Whatman £1) for a 24-h period. Crickets had been fed ad libitum a commercially prepared dry dog food. *P. milvina* were field collected and maintained on a diet of *Drosophila hydei* for at least 2 wks prior to introduction on filter paper. Crickets were slightly larger in size than *P. milvina* but not significantly so (mean cricket wt. = 36.3 mg  $\pm$  SE 0.0143; mean *P. milvina* wt = 20.3 mg  $\pm$  SE 0.0006;  $t_{14} = 1.12$ ,  $p = 0.281$ ).

### Testing Protocol

Both prey filter paper treatments were presented simultaneously to individual *H. helluo* that had been maintained on crickets or *P. milvina*. The testing arena was a 20-cm diameter, 8 cm high plastic container. The two treated half circles of filter paper collectively covered most of the bottom surface area except for a 2-cm

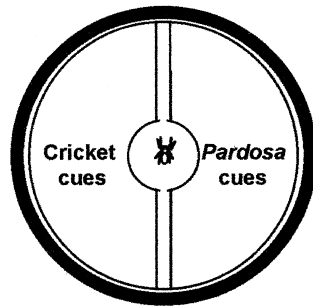


Fig. 1: The arena used for spider testing. Spiders are placed in the center of the arena under a vial and allowed to move between stimulus treatments for a 1-h period after a 1-min acclimatization period

band that separated the sheets (Fig. 1). In addition, a half circle was cut in the center of each sheet so there was an untreated area into which we could introduce the spider (Fig. 1). One half-circle sheet of filter paper contained chemical cues from crickets, the other contained cues from *P. milvina*. The position of each sheet was randomized for each spider treatment to control for any side bias present within the test arena.

For each experimental trial, a single *H. helluo* spider was introduced in the center of the arena within an inverted clear plastic vial. Spiders were allowed to acclimatize for 1 min after which the vial was removed and the spider was free to move between the two sheets of paper for 1-h. The test arena was rinsed with 95% ethanol between trials and allowed to dry to remove all residual odor cues. All spiders were tested between 0700 and 1900 h. For each spider, we recorded the following behaviors for each filter paper treatment: 1. time spent moving forward (locomotion); 2. time spent in non-forward locomotion (defined as any movement of the appendages or turning of the body in place without forward movement); 3. time spent immobile (no visible indications of movement); 4. distance traveled (cm) (5) speed (distance moved/time spent moving forward), and (6) residence time (time spent on filter paper). We also recorded the initial choice of sides for each pairing.

We measured locomotor behavior by monitoring the spiders remotely using an automated digital data collection system (Videomex-V, Columbus Instruments, Columbus, OH, USA) connected to a video camera (JVC high band Saticon GXS 700).

All behaviors were recorded automatically and downloaded to a continuous-feed printer. The Videomex-V system converts contrasting images to pixels (dark spider on a white paper background) and records and computes changes in pixel positions over time. Changes in spider movement were recorded every second and required a movement of at least one body length in the period to be measured as forward movement. All locomotor patterns were outputted to the printer every 5 min and all locomotor behaviors were summed over 1 h. All data approximated a normal distribution based on a Wilks–Shapiro Rankit test for normality. Paired

t-tests were used to compare differences within the paired treatments for each type of locomotor behavior;  $\chi^2$  goodness-of-fit tests were used to determine significant differences in the initial choice of sides in each treatment pairing.

### Results

*H. helluo* fed crickets did not initially choose one side of the arena significantly more than the other ( $\chi^2$  goodness of fit = 1.20,  $p = 0.2733$ ). However, *H. helluo* fed *P. milvina* initially chose the *P. milvina* side of the arena significantly more often than would be expected by chance ( $\chi^2$  goodness of fit = 6.53,  $p = 0.01$ ).

Spiders that had eaten *P. milvina* 9 d earlier spent significantly more time on the *P. milvina* side of the arena ( $n = 15$ , paired  $t_{14} = -2.34$ ,  $p = 0.035$ ), whereas *H. helluo* that had eaten crickets 9 d earlier spent significantly more time on the cricket side of the arena ( $n = 15$ , paired  $t_{14} = 2.39$ ,  $p = 0.031$ ) (Fig. 2). Differences in residence time appear to be attributed primarily to significantly more time spent immobile on those substrates. Although both *H. helluo* diet treatment groups exhibited significantly more time immobile on the side of the arena previously occupied by their most recent prey, the duration of time spent immobile appeared larger for *H. helluo* fed crickets compared with *H. helluo* fed *P. milvina*. *H. helluo* fed crickets spent approximately six times the amount of time immobile on the cricket side of the arena than the *P. milvina* side. Spiders fed *P. milvina* spent nearly twice as long immobile on the *P. milvina* paper treatment than on the cricket treatment side. Average speed was not significantly different between prey substrates for *H. helluo* fed crickets (paired  $t_{14} = -0.96$ ,  $p = 0.35$ ). Spiders fed crickets moved an average of  $3.83 \pm 0.33$  cm/s on the cricket substrate and  $3.82 \pm 0.22$  cm/s

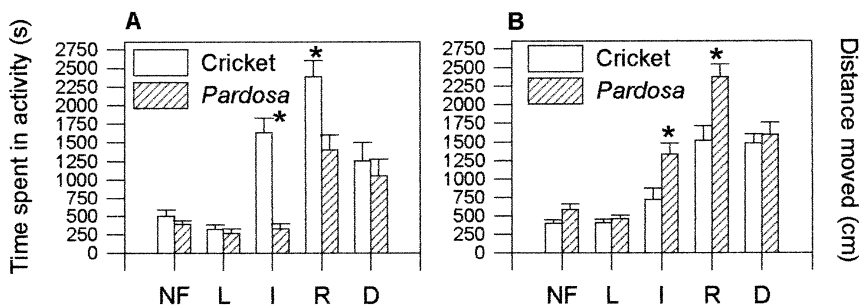


Fig. 2: Locomotor patterns of adult female *Hogna helluo* exposed to paired treatments of filter paper previously occupied by either a single domestic cricket nymph (*Acheta domesticus*), or an adult female *Pardosa milvina* for 24 h. Behavioral categories on ordinate are as follows: NF = non-forward locomotion, L = forward locomotion, I = immobility, R = residence time, D = distance moved. Distance moved is measured in cm, but on the same scale as s. All other behaviors are measured in s. Results are shown as means ( $n = 15/\text{treatment}$ )  $\pm$  SE. Asterisks denote significant differences between treatment pairs at the 0.05 level based on paired t-tests. A = responses of *H. helluo* fed crickets, B = responses of *H. helluo* fed *P. milvina*

on the *P. milvina* substrate. However, *H. helluo* fed *P. milvina* showed a marginally nonsignificant difference in average speed (paired  $t_{14} = -1.94$ ,  $p = 0.07$ ). Spiders fed *P. milvina* moved an average of  $4.13 \pm 0.43$  cm/s on the cricket substrate, but slowed to a mean of  $3.58 \pm 0.22$  cm/s on the *P. milvina* substrate. For both diet treatments, spiders tended to move more slowly on the substrate containing cues associated with recent prey. No other category of locomotor behavior was significantly different between filter paper treatment pairings. *H. helluo* fed *P. milvina* tended to spend longer periods of time in non-forward locomotion on the *P. milvina*-treated paper (paired  $t_{14} = -2.01$ ,  $p = 0.063$ ), but the difference in time spent in non-forward locomotion was smaller between treatments for *H. helluo* fed crickets (paired  $t_{14} = 1.41$ ,  $p = 0.181$ ; Fig. 2).

### Discussion

Residence time biases on different substrates are consistent with the previous diet of *H. helluo*. Results suggest that *H. helluo* is capable of remembering the type of food it has eaten most recently and shows foraging preferences for those food types even after 9 d without food. Although spiders were deprived of food for 9 d, they were maintained in the same container in which they were fed. Chemical cues from prey in the containers may have persisted for some time after their last feeding and may have facilitated association of the cues with their container as well as prey.

The difference in the magnitude of preference between the two treatment groups may be partly attributed to a bias in feeding neophobia among *H. helluo* fed crickets (tendency to avoid unfamiliar prey). *H. helluo* fed crickets had never encountered *P. milvina* chemical cues before and may have shown an aversion to unfamiliar *P. milvina* cues in addition to a preference for cricket cues. *H. helluo* fed *P. milvina* had been maintained on a diet of crickets as recently as 39 d earlier. Therefore, *H. helluo* fed *P. milvina* may not have had neophobia toward cricket prey or may have had a memory of feeding on crickets previously as well. For several species of natracine snakes, there is evidence of food imprinting and genetically based prey preferences (reviewed in Burghardt 1993), whereby prey preferences may be innate. The cricket-fed *H. helluo* used in this experiment was from a population that regularly feeds on *P. milvina*. However, *H. helluo* naive to *P. milvina* showed no obvious innate bias toward *P. milvina* chemical cues. Although the magnitude of responses toward each prey type was different, there did not appear to be large qualitative differences in locomotor behaviors between *H. helluo* maintained on different diets. Although spiders showed chemically mediated prey preferences, their movement patterns with respect to non-forward locomotion, distance traveled, and forward locomotion were similar. This suggests that the foraging strategy for both prey types in response to chemical cues alone is the same.

*H. helluo* had longer residence times and longer periods of immobility while on substrates previously occupied by prey from their recent diet. Many animals show increased localized searching in the presence of chemical cues from food

rather than decreased locomotion (Bell 1991). The counterintuitive response of decreased mobility exhibited by *H. helluo* may be explained by the general foraging strategy of these spiders. Most wolf spiders are sit-and-wait predators that remain motionless in a foraging patch for a period of time before leaving (Ford 1978). *H. helluo* are especially likely to remain in foraging areas for long periods of time since they are facultative burrowers (Walker et al. 1999a). Also, activity levels of *H. helluo* are known to be affected by recent feeding history. When well fed, as in this study, spiders adopt a more sit-and-wait foraging strategy. With increasing hunger level, they become more active searchers (Walker et al. 1999b). As such, immobility on a particular substrate may be interpreted as a choice of foraging site rather than searching behavior. Studies have shown that the wolf spider *Schizocosa ocreata* exhibit long periods of immobility in the presence of visual and vibratory stimuli from prey (Persons & Uetz 1996b, 1997a, 1998). However, with *S. ocreata*, there is no evidence that prior sensory experience with visual or vibratory cues from insect prey affects subsequent residence time duration in patches (Persons & Uetz 1996b), even when spiders were previously fed prey in the patch (Persons & Uetz 1997b). Results reported here suggest that *H. helluo* can learn to associate indirect cues, perhaps silk, feces or some other cue with a particular prey type and modify their residence time on that substrate accordingly.

Given the initial side preference of *H. helluo* fed *P. milvina* and the presence of silk draglines produced by *P. milvina*, we suggest that the types of chemical cues used by *H. helluo* to detect each prey type may be quite different. *H. helluo* fed *P. milvina* showed an initial bias for the *P. milvina* side of the arena, yet *H. helluo* fed crickets did not show a corresponding bias. This suggests that *P. milvina* females may emit volatile odor cues that *H. helluo* can learn to recognize. Recent field and laboratory studies have found that *P. milvina* females emit an airborne pheromone toward males (Searcy et al. 1999) and it is plausible that *H. helluo* may be exploiting this communication channel to increase foraging success. We cannot refute the possibility that *H. helluo* can distinguish between silk and/or feces of each prey type based on visual information alone rather than volatile kairomones, but behavioral studies of wolf spider visual perception suggest that nonmoving objects are not easily perceived (Rovner 1996). Further, both feces and silk would probably provide low contrast on a white sheet of paper. Although there is evidence that some species of spider respond to airborne pheromones (Watson 1986; Tietjen 1979), to our knowledge, there are no previous studies that suggest spiders respond to airborne chemical cues from prey. Jackson (1995) found that jumping spiders in the genus *Portia* are unresponsive to volatile chemicals produced by prey spiders. However, olfactory cues from conspecifics will inhibit foraging behavior and prey attack (Willey & Jackson 1993).

It remains unclear what role associative learning of chemical cues plays in prey detection and foraging decisions under natural conditions since it is largely unknown if or how often particular spiders switch prey types. However, the strength of response after a long period without food suggests that indirect prey cues may be used frequently among spiders to choose foraging sites. The strength of the prey cues used for this study may be artificially high but is probably considerably less

than previous studies testing spider reactions to prey cues. Here, only a single prey item was allowed to walk on the stimulus filter paper for 24 h. Punzo & Kukoyi (1997) maintained individual prey on the paper for 72 h, and Persons & Uetz (1996a) used 100 crickets for a 30-min period. Given studies that suggest wolf spiders may suffer fitness consequences from a monotypic diet (Greenstone 1979; Uetz et al. 1992), it is surprising that spiders show biased prey preferences. It is possible that spiders encounter chemically defended, spined, or otherwise difficult to eat prey with sufficient frequency, that palatable prey may elicit associative prey preferences.

The ability to associate indirect cues with particular prey may facilitate the spider's assessment of foraging patch quality. *P. milvina* densities may be high within the soybean fields used as collecting sites, approaching 5 individuals/m<sup>2</sup> (S. Marshall & A. L. Rypstra, pers. comm.). Since some species of wolf spider are capable of assessing prey density with sensory information only and modifying residence times in particular food patches accordingly (Persons & Uetz 1998), results reported here suggest that *H. helluo* may frequently encounter *P. milvina* or other prey types previously consumed and choose foraging sites based on this information. Future studies that examine spider responses to different natural prey types may be fruitful.

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