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CHEMOSENSORY RESPONSE TO PREY IN *PHIDIPPUS AUDAX* (ARANEAE, SALTICIDAE) AND *PARDOSA MILVINA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. Many predators exploit the chemical signatures of prey when foraging. We present a comparative study designed to test if the foraging behavior of *Phidippus audax* (Hentz 1845) is manipulated by substrate-borne chemicals left by prey. Our findings suggest that foraging *P. audax* do not use chemical cues left by prey, while the wolf spider *Pardosa milvina* (Hentz 1844) in the same experimental setup does respond to chemical cues. However, further examination into the role of chemical cues on prey detection in salticids is required.

Keywords: Salticidae, Lycosidae, foraging, chemical cues

The sensory adaptations used to locate prey are diverse, varying with foraging strategy and elements of the environment (Cooper 2000). The ability to use chemical stimuli to detect prey has been found in both vertebrates (e.g., Burghardt 1973; Arnold 1981; Dittman et al. 1998; Nevitt 2000; Rangen et al. 2000) and invertebrates (e.g., Rebach 1996; Hori 1999, Mondor & Roitberg 2000) including spiders (Persons & Uetz 1996; Punzo & Kukoyi 1997; Persons & Rypstra 2000). Nevertheless, the use of chemical cues as a mechanism for detecting prey remains understudied in spiders and further investigation into its role is critical to our chances of understanding their foraging decisions.

We report a test of the hypothesis that *Phidippus audax* (Hentz 1845)(Araneae, Salticidae) uses chemical cues of prey to adjust its foraging behavior. The foraging behavior of ant-eating jumping spiders, *Habrocestum pulex* (Hentz 1846), has been found to be influenced by chemical cues from prey (Clark et al. 2000). However, it is assumed that this species is monophagous and, thus, may have a heightened ability to respond to the chemical signature of its prey, while a generalist predator, such as *P. audax*, may not. Moreover, the cannibalistic jumping spider *Portia labiata* (Thorell 1887) appears to possess the ability to distinguish chemically between its own and conspecific egg sacs. Because this species is disposed to consume conspecific egg sacs, perhaps we may interpret this as chemical discrimination between prey (Clark & Jackson 1994).

Specifically, our aim was to examine the effects of substrate-borne chemical cues of prey on the amount of time invested in a given patch in *P. audax*. We compared our results (and tested our protocol) using the wolf spider *Pardosa milvina* (Hentz 1844)(Araneae, Lycosidae), because other wolf spiders have been demonstrated to respond to chemical prey cues on substrates (Persons & Uetz 1996; Persons & Rypstra 2000). *Phidippus audax* and *P. milvina* are excellent subjects to use in a comparative investigation as they are syntopic, cursorial, diurnally active, generalist predators, and employ both ‘sit-and-wait’ and ‘active’ foraging strategies (Givens 1978; Walker et al. 1999). However, because jump-

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ing spiders are renowned for their exceptional visual acuity, an intriguing contrast emerges that may separate them from other spiders in the nature of cues used in prey detection.

We captured all spiders (of both species) in the field in Amherst and Leverett, Massachusetts during the summer of 2000. All were kept in the laboratory for 2–6 weeks prior to testing. They were housed in plastic cages on a 13:11 light:dark cycle at approximately 26 °C. Once per week, we provided spiders with approximately five crickets (*Acheta domesticus*, Top Hat Cricket Farm, Kalamazoo, Michigan), which allowed spiders to feed to satiation. We provided water *ad libitum* in test tubes plugged with cotton. Prior to testing, spiders were starved for 10–15 days to ensure that they were hungry. Voucher specimens were deposited in the University of Massachusetts Department of Entomology insect collection.

Experiment 1, conducted on *P. audax* only, was a simultaneous choice test between two filter papers, one that had been exposed to crickets and one that had not. This protocol has been used previously in studies of wolf spider response to chemical prey cues (Persons & Uetz 1996, Persons & Rypstra 2000). We placed experimental filter papers (11 cm diameter) in petri dishes for 48–72 h with approximately 5–10 medium-sized juvenile crickets. Control papers were placed in petri dishes with no crickets.

The test arenas were clear plastic boxes (30 × 23 × 11 cm high). Between trials, the boxes were washed with soap, soaked in a diluted bleach solution for at least 10 min, rinsed, and wiped down with ethyl alcohol to reduce potential odor cues. The bottom of the box was divided into thirds. We randomly assigned treated and untreated filter papers to either side, leaving the middle neutral area open. To minimize potential visual disturbance, boxes were placed inside a large Rubbermaid® plastic storage bin (50 × 34 × 22 cm high) covered with opaque white paper.

Experiments were conducted in a quiet room during daylight hours under fluorescent light, between 22–25 °C. We placed each spider inside a large syringe with the top cut off and plugged the open end with a ball of tissue paper. The tip was placed through a hole in the side of the box near the center of the neutral area. We gave each spider a 5 min acclimation period in the syringe, and then removed the tissue paper and slowly pushed the syringe plunger to move the spider into the arena. Timing started as soon as the spider was released. Two digital timers were used to record the spider's activity. Because we were interested in whether spiders could detect cues when close to or touching the filter paper, we recorded both the time spent on each filter paper and the time spent in the third of the arena in which each paper was located. We observed each spider for 20 min. Each spider was given one trial.

It is possible that salticids may need to make physical contact with the substrate in order to detect chemical cues. However, spiders did not always sample both filter papers in experiment 1. We therefore designed experiment 2, a sequential presentation, where spiders were placed directly on a piece of filter paper that covered half of the bottom of the arena. We noted the time spent on or off the filter paper. We tested each spider twice, once with treated and once with untreated paper. The order of the presentation of filter papers was randomly assigned. In all other respects, this protocol was identical to experiment 1.

We tested 13 adult *P. audax* in experiment 1 and 15 in experiment 2, mostly females with several males in each test. We tested *P. milvina* only in experiment 2 ($n = 15$, 9 adult female, 6 adult male). Data were analyzed with Wilcoxon signed rank tests.

We found no evidence that *P. audax* distinguished between control and experimental filter papers. In experiment 1, there was no difference in the amount of time spiders spent on the untreated vs. the treated filter paper (Wilcoxon signed rank test, tied $Z = -0.105$, $p > 0.9$, $n = 13$, Fig. 1a). There was also no difference in the amount of time spiders spent in the third of the arena with the untreated paper vs. the third with the treated paper (Wilcoxon signed rank test, tied $Z = -0.549$, $p > 0.5$, $n = 13$). In experiment 2, we found no difference in the amount of time spiders spent on the control filter paper vs. the treated paper (Wilcoxon signed rank test, tied $Z = -0.369$, $p > 0.7$, $n = 15$, Fig. 1b). In contrast, *P. milvina* spent significantly more time on the treated filter paper than the untreated paper (Wilcoxon signed rank test, tied $Z = -3.237$, $p < 0.002$, Fig. 1c).

Pardosa milvina appear to possess chemo-

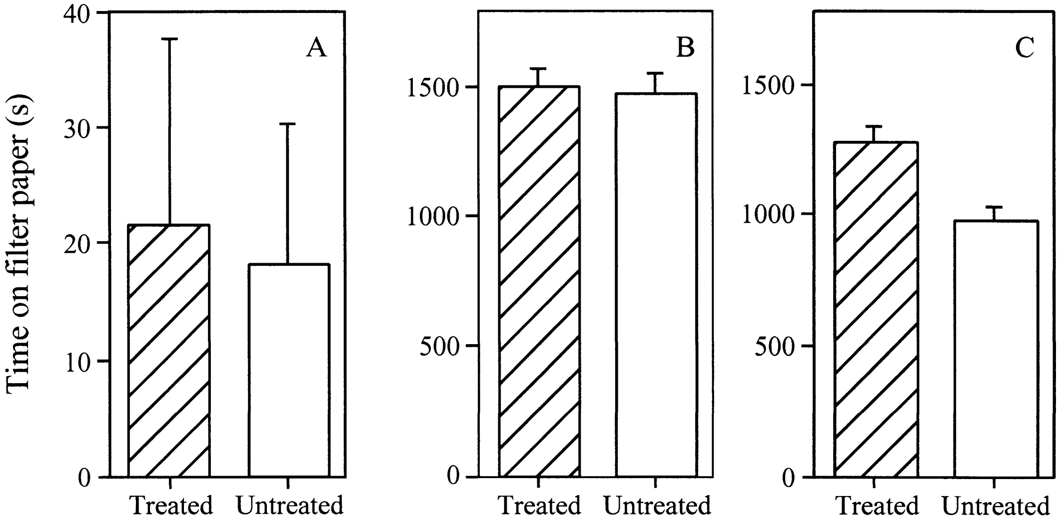

Figure 1.—The amount of time spent on cricket-treated vs. untreated filter paper. (A) Simultaneous presentation of both types of filter paper to *P. audax*. (B) Sequential presentation of both types of filter paper to *P. audax*. (C) Sequential presentation to *P. milvina*.

sensory ability. This finding is consistent with previous investigations of wolf spiders (Persons & Uetz 1996; Persons & Rypstra 2000). We frequently observed *P. milvina,* but not *P. audax*, passing their legs and palpal tarsi through the chelicerae as well as biting the edges of the cricket-treated filter paper substrata. We did not see these behaviors in trials with untreated filter paper substrata. This suggests that perhaps in addition to other chemical (e.g. olfactory) cues, gustatory cues may be important in the prey locating abilities of wolf spiders. However, we agree with the caution expressed by Persons & Uetz (1996) that because treated filter paper was exposed to large numbers of crickets over a period of days, the degree to which these spiders react to chemical cues of prey may be inflated in our study compared to natural situations.

Foraging patch residence times did not differ whether cricket-treated or untreated filter paper was used in *P. audax* trials. This is consistent with expectation if *P. audax* cannot or does not use chemical stimuli to locate prey. Jumping spiders depend strongly on visual cues of movement, size, and shape to capture prey (Land 1971; Dill 1975), and *P. audax* has been demonstrated to use species-specific visual cues to select and avoid potential prey (Freed 1984). Perhaps as a consequence of the evolution of exceptional visual faculties, chemosensory response to prey has abated. Some other highly visual species do not respond to chemical cues. For example, predatory water bugs *Microvelia macgregori* (Hemiptera, Veliidae) respond to visual and vibrational but not chemical cues during prey detection (Jackson & Walls 1998). Interestingly, lycosids also visually detect the movement of prey (e.g., Rovner 1993, Persons & Uetz 1998). This suggests that the difference we found between the species is not simply because *P. milvina* is incapable of visual prey detection.

At present, we are not prepared to suggest that *P. audax* lacks the ability to perceive chemical cues left by prey but that they do not react similarly to *P. milvina*. Perhaps *P. audax* perceives chemical cues of prey and subsequently responds by attempting to locate them visually as opposed to investing longer periods of time at the source engaging in overt gustatory or olfactory behaviors. It is important to note that *P. audax* does use chemical cues in the context of mating. For example, Oden (1981) demonstrated that adult male *P. audax* responds to chemical cues left by adult and sub-adult female conspecifics. Thus, we should be cautious not to prematurely reject any role for chemical cues in the context of foraging in *P. audax*, but this piece of evidence suggests that the role is less than for lycosids.

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