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Dragline deposition patterns among male and female *Hogna helluo* (Araneae, Lycosidae) in the presence of chemical cues from prey

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Abstract. Prey are able to show adaptive antipredator responses in the presence of silk from the wolf spider *Hogna helluo* (Walckenaer 1837). *Hogna helluo* also is attracted to chemical cues associated with previously consumed prey. Consequently *H. helluo* may benefit by modifying its silk deposition when encountering prey cues to avoid detection. Silk is an important medium for female wolf spiders to attract prospective mates, whereas silk is putatively less important for males to attract females. Females also consume much more food than males after maturity; therefore, male and female *H. helluo* may differ in the relative costs and benefits of silk deposition with respect to improved feeding efficiency. We tested whether field-caught male and female *Hogna helluo* changed silk deposition patterns in the presence of excreta deposited by domestic crickets, *Acheta domesticus*, (Linnaeus). Hungry male and female *H. helluo* were allowed to deposit silk for four hours in containers either previously occupied by five crickets for 24 h or devoid of cues ($n = 36$). We found no significant decrease in silk dragline deposition among males or females in the presence of prey cues; however, female spiders showed a significant decrease in the number of attachment disks produced in the presence of cricket cues whereas males did not. Our results suggest that *Hogna helluo* do change silk deposition patterns in the presence of crickets, but that these changes are sex-specific.

Keywords: Draglines, anti-predator, crickets, kairomone, wolf spider

All species of spider putatively produce silk draglines as they move through their environment. These threads serve as an important communication medium among spiders (reviewed by Schulz 2004; Huber 2005; Gaskett 2007). Some species discriminate between conspecific and heterospecific silk (Roland 1984). Others are able to assess fighting ability (Clark et al. 1999) or mating status of conspecifics using only information associated with draglines (Rypstra et al. 2003; Schulz 2004; Roberts & Uetz 2005).

Draglines from the major ampullate glands may potentially be an important source of information for both predators and prey of spiders (Schulz 2004). Recent studies have found that the wolf spider, *Pardosa milvina* (Hentz 1844), is capable of extracting information about predator risk via silk and other metabolic products from a larger co-occurring wolf spider, *Hogna helluo*. From chemical cues alone, *Pardosa milvina* can extract information about size (Persons & Rypstra 2001), diet (Persons et al. 2001), and hunger level (Bell et al. 2006) of *H. helluo* as well as how recently it has been in the area (Barnes et al. 2002). This information is then used to effectively avoid predation by *H. helluo*. Similarly, spiderlings of *Rabidosa rabida* (Walckenaer 1837) reduce activity and show avoidance behavior when encountering silk of adult female *P. milvina* (Eiben & Persons 2007). A number of insect species are also capable of detecting silk and other cues associated with spiders and responding with antipredator or avoidance behavior. Japanese beetles (*Popillia japonica* Newman 1841) and Mexican bean beetles (*Epilachna varivestis* Mulsant 1850) reduce herbivory on soybeans previously walked on by the wolf spiders *H. helluo*, *Rabidosa rabida* (Walckenaer 1837), or *P. milvina* (Hlivko & Rypstra 2003) and the field cricket, *Gryllus integer* (Scudder 1901) reduces activity and avoids substrates containing chemical cues associated with the funnel-web spider *Hololena nedra* (Chamberlin & Ivie 1942) if *H. nedra* have previously fed on *G. integer* (Kortet & Hedrick 2004).

Given that spider silk and other metabolic products are known to be used by prey to alert them to the presence of a predator, it may be adaptive for spiders to modify silk deposition during foraging if they are capable of detecting and responding to chemical cues associated with prey. A number of spider species are capable of detecting and preferentially foraging in areas where chemical cues or metabolic waste products from prey are found. The wolf spider *Hogna helluo* shows a marked preference for substrates previously occupied by crickets or the smaller co-occurring wolf spider, *Pardosa milvina* (Hentz 1844), when previously fed crickets or *P. milvina* respectively (Persons & Rypstra 2000). Similar diet-based preferences for substrates with prey cues have been found in the wolf spider *Hogna carolinensis* (Walckenaer 1805) (Punzo & Preshkar 2002), *Trochosa parthenus* (Chamberlin 1925), and the oxyopid, *Oxyopes salticus* (Hentz 1845) (Punzo & Kukoyi 1997). The zoodariid ant-specialist, *Habronestes bradleyi* (Cambridge 1869) is attracted specifically to the alarm pheromones of the meat ant *Iridomyrmex purpureus* (Smith 1858) (Allan et al. 1996) and the wolf spider *Schizocosa ocreata* (Hentz 1844) is attracted to substrates previously occupied by the cricket *Acheta domesticus* (Persons & Uetz 1996).

Since adults of the wolf spider, *H. helluo*, are known to change foraging behavior when detecting prey chemical cues and prey show antipredator responses when detecting substrates with *H. helluo* silk, we hypothesized that *H. helluo* should modify their silk deposition when detecting chemical cues from prey. However, the relative fitness trade-offs for modifying silk deposition while foraging may be different for males and females. Adult female *H. helluo*, like most lycosids, are larger, more rapacious, and gain weight quickly relative to males (Walker & Rypstra 2001; Lehmann et al. 2004). Therefore, females benefit more by improved foraging

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efficiency (Walker & Rypstra 2002). However silk may also be used by females to advertise to males their willingness to mate and, thus, there may be an opportunity cost associated with stopping silk deposition among females but not males. Here we compared changes in silk deposition of adult male and female *H. helluo* when detecting chemical cues associated with prey and predicted that females would show a greater shift in silk deposition behavior than males. If cricket antipredator responses to spider silk are especially effective, females should dramatically reduce silk production when encountering cricket chemical cues. Alternatively, if females use silk to mark and subsequently navigate around foraging patches likely to contain prey and prey responses to silk are weak, then females should increase silk deposition when detecting prey cues.

METHODS

Spider collection and maintenance.—Male and female *Hogna helluo* were collected in agricultural fields in Snyder County, Pennsylvania. Spiders were housed individually in 9 cm diameter, 7 cm high opaque containers. Each container was filled with 2–3 cm of moistened peat moss that served as a water source and means of maintaining humid conditions within the container. To familiarize spiders with cricket prey and minimize the effects of prior feeding experiences on silk deposition responses, spiders were fed weekly 2–3 domestic house crickets, *Acheta domesticus* (L.) for 3 wk prior to testing. Water was added to containers ad libitum to maintain a moist environment.

Substrate and trial container preparation.—Sheets of paper were prepared as substrates prior to testing. Each sheet was printed with an 80 mm diameter circular grid. Each paper substrate was prepared by printing a white on black alphanumerically coded 2.5 mm grid pattern onto each sheet of standard copy paper. These grids were cut out and stored until use in an air tight container. Latex gloves were worn and scissors were wiped with ethanol to prevent contamination. Each grid was taped into a 9 cm diameter, 7 cm high opaque container.

Experimental design.—*Hogna helluo* spiders were fed 2–3 domestic house crickets once a week for 3 wk prior to testing. Ten days prior to the start of the experiment all food was removed and feeding was stopped until after testing. Water continued to be provided as needed. Spiders were randomly assigned to cricket cue or control groups in equal numbers. Containers in the cricket cue treatment were prepared by placing 5 adult male and female *Acheta domesticus* on prepared substrates for 24 h. Crickets were then removed and treatment spiders were transferred into testing containers using a plastic 166 ml (= 45 dram) vial. Control spiders were placed into prepared testing containers void of any cricket cues. After 4 h in testing containers, spiders were carefully removed so as to not disturb deposited silk. Spiders were returned to their respective housing containers. Returned spiders were then fed 2–3 crickets and all experimental procedures were repeated with individual spiders being switched between control and cricket-cued treatments. Results were analyzed using repeated-measures ANOVA with sex and prey cue as factors.

Silk quantification.—Testing containers were examined using a Meiji EMZ-5 Stereo microscope. Silk was quantified using two methods. Silk draglines were counted by the number of squares that were covered with 50% or more silk. We also counted the total number of attachment disks deposited on the gridded sheets.

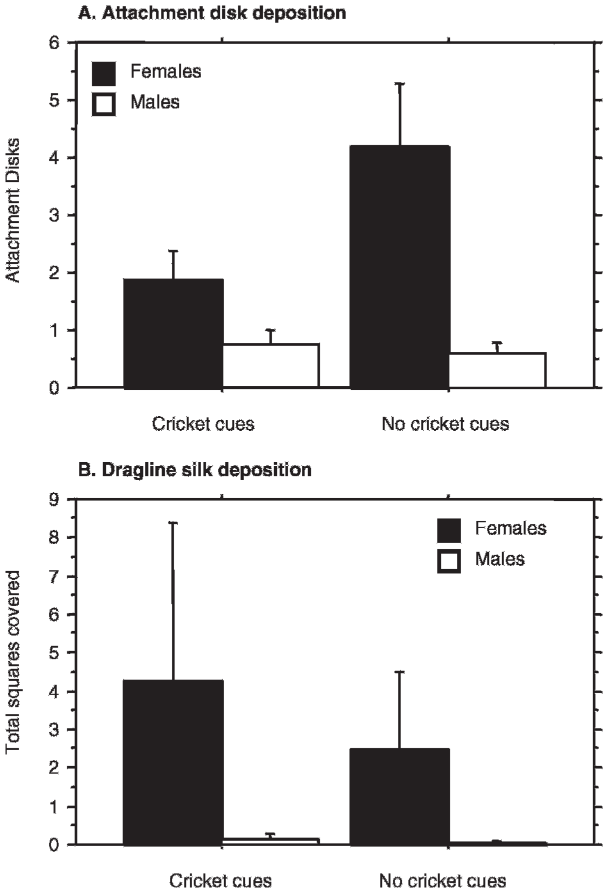

Figure 1.—A. Mean number of attachment disks deposited by male and female *H. helluo* (+ S.E.) while on clean sheets of paper (no cricket cues) or sheets of paper previously occupied by five crickets (*Acheta domesticus*) for 24 h (cricket cues). B. Total number of squares with at least 50% silk dragline deposition by male and female *H. helluo* (+ S.E.) while on clean sheets of paper (no cricket cues) or sheets of paper previously occupied by five crickets (*Acheta domesticus*) for 24 h (cricket cues).

RESULTS

We found a significant difference in attachment disk deposition between males and females (ANOVA: Sex = $F_{1,34}$ = 12.970 ; P = 0.001). We also found a significant effect of prey cue presence on attachment disk deposition (Repeated Measures ANOVA: Prey Cue = $F_{1,34}$ = 5.989 ; P = 0.0197) as well as a significant prey cue and sex interaction (Prey Cue * Sex = $F_{1,34}$ = 7.766 ; P = 0.0086; n = 36; Fig. 1A). Females produced about twice as many attachment disks as males while in the presence of prey cues and over four times as many in the absence of prey cues. Total quantity of dragline silk did not differ significantly by sex or the presence of prey cues (Repeated Measures ANOVA: Sex = $F_{1,34}$ = 1.453 ; P = 0.2346 ; Prey Cue = $F_{1,34}$ = 0.856 ; P = 0.3506 ; Prey Cue * Sex = $F_{1,34}$ = 0.713; P = 0.4045; n = 36; Fig. 1B).

DISCUSSION

Male and female *H. helluo* varied dramatically in the quantity of dragline and attachment disks deposited on the substratum. Females produced large amounts of dragline silk while males produced negligible amounts. Despite a seven-fold difference in mean dragline silk deposited by males and females, there was no statistically significant difference in the amount deposited. This is attributable mostly to high variability in female silk deposition behavior compared to males. Females also produced a greater number of attachment disks relative to males. The significant difference in attachment disk deposition between males and females may be the result of general differences in the role of silk in intersexual communication. The differences in deposition between sexes suggest that female *H. helluo*, like other lycosids, use dragline silk to attract males while males do not use draglines to attract females (reviewed in Schulz 2004). As originally predicted, our results indicate that males do not make any significant tradeoffs between mate advertisement and compromised foraging within the context of silk production. Dragline silk deposition was highly variable among females. Attachment disks, produced by the pyriform glands of the anterior spinnerets (Dijkstra 1976), were often associated with fine gauge silk deposition, but it also appeared that females were capable of producing attachment disks in the absence of dragline silk. This suggests that attachment disks may have some function other than dragline fixation to the substratum. Dijkstra (1976) showed that male wolf spiders are capable of using attachment disks to gather information about the directional heading of females. If this finding is generally applicable to lycosids, attachment disk deposition by female *H. helluo* may be important in attracting males.

Our results are consistent with the hypothesis that females may reduce attachment disk deposition, but not dragline silk, to evade detection by prey. However there may be alternative explanations for this. Attachment disk reduction could be a by-product of reduced activity when encountering prey cues on a substrate. Female *H. helluo* activity drops dramatically when encountering substrates with cricket cues (Persons & Rypstra 2000) as might be expected from a sit-and-wait predator. When encountering cricket cues *H. helluo* typically switch to short bouts of walking and long periods of immobility relative to substrates without these cues. During pauses, *Hogna helluo* appeared to increase pivoting behavior on these cricket substrates, suggesting that the spiders were visually surveying the area for movement. If attachment disks are deposited primarily during pauses or stops after walking bouts, we would have expected increases in attachment disk deposition rather than decreases. Since it remains unknown if attachment disk and dragline silk deposition are tightly correlated to movement, we cannot eliminate the possibility that reductions in attachment disk deposition is a simple by-product of reductions in overall movement.

Acheta domesticus is an introduced species but has persisted in the eastern United States for some time (Blatchley 1920; Ghouri 1961). However *H. helluo* may not necessarily show as strong a behavioral response to chemical cues from it as the more common co-occurring species in central Pennsylvania, *Gryllus pennsylvanicus* (Burmeister 1838). *Hogna helluo* used in our study were fed a diet of *A. domesticus* for three weeks prior to testing. Previous studies have shown that this is sufficient time to induce a substrate preference for chemical cues associated with *A. domesticus* (Persons & Rypstra 2000) and thus enhance any foraging-related shifts in silk deposition.

It is currently unknown if *Acheta domesticus* display antipredator responses toward attachment disks and/or dragline silk, so it remains unclear if such shifts in silk deposition are adaptive. However other species of cricket do show adaptive antipredator responses to spider chemical cues (Kortet & Hedrick 2004), suggesting that *A. domesticus* may as well. Our results do not support the possibility that female *H. helluo* mark foraging areas likely to contain large numbers of prey by increasing silk deposition in areas with prey cues.

We did not measure shifts in defecation behavior in *H. helluo* but this too could be a significant source of chemical information for prey. The cricket, *Gryllus integer*, showed avoidance behavior of chemical cues from funnel-weaving spiders but only when these spiders were fed a diet of *G. integer*. Such diet-based information could originate from silk, excreta, or both. Morse (in press) found that adult female crab spiders, *Misumena vatia* (Clerck 1757), do not defecate near their hunting sites and selectively move to the distal portion of leaves when defecating. This could be done to limit attacks by parasitic wasps or parasites, but it may also reduce antipredator responses from insects that may respond to excreta from spiders.

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