Journal of Insect Behavior (© 2006)
DOI: 10.1007/s10905-005-9008-x

The Influence of Pedipalp Autotomy on the Courtship and Mating Behavior of *Pardosa milvina* (Araneae: Lycosidae)

Erin C. Lynam,[1] J. C. Owens,[1] and Matthew H. Persons[1,2]

Revised August 26, 2005; accepted September 7, 2005

Male Pardosa milvina *wolf spiders use their pedipalps both for copulation and courtship. Pedipalp loss is significantly more common among adult males compared to females. We measured the courtship and mating effects associated with the loss of one or both pedipalps among adult male* P. milvina. *Pedipalp loss significantly reduced courtship intensity, but had no influence on mounting success. Intact males were less likely to be cannibalized and suffered fewer predatory attacks by females than autotomized males. Loss of the left pedipalp resulted in significantly less intense courtship, higher female aggression levels, and delayed onset of courtship whereas loss of the right pedipalp minimally affected male and female behavior relative to intact males. Pedipalp displays may function in reducing female aggression rather than increasing female receptivity.*

KEY WORDS: *Pardosa milvina*; pedipalp; courtship; wolf spider; lycosidae; mating success.

INTRODUCTION

Spiders exhibit sexual dimorphism in their anterior-most appendages, pedipalps. Among adult females and juveniles, these limbs are used most often to facilitate prey capture, manipulation, and consumption. In adult males, pedipalps are highly modified as copulatory organs for sperm

[1]Biology Department, Susquehanna University, 514 University Avenue, Selinsgrove, Pennsylvania 17870.
[2]To whom correspondence should be addressed; e-mail: persons@susqu.edu,.

transfer. Male pedipalps also possess chemosensory hairs used to locate receptive females through pheromone detection and dragline following and, in many species, are waved, rotated, drummed, or rubbed as part of courtship displays (Montgomery, 1903; Kaston, 1936; Rovner, 1967). In some species, they may also be brightly colored or covered in decorative setae relative to female pedipalps. Consequently, in addition to their obvious role in sperm transfer, pedipalps are likely to be important for locating potential mates and possibly conveying information to the female about species identity or male quality prior to mating.

Leg loss due to predator avoidance, conspecific aggressive interactions, or general injury is a common phenomenon among wolf spiders, occurring in more than 30% of spiders in some field populations (Brueseke *et al.*, 2001; Brautigam and Persons, 2003). The foraging, predator avoidance, and mating costs of leg autotomy have been well quantified in lycosids as well (Klawinski and Formanowicz, 1995; Uetz *et al.*, 1996; Amaya *et al.*, 2001; Brueseke *et al.*, 2001; Brautigam and Persons, 2003). However, we are unaware of studies that have recorded the frequency of pedipalp loss among field populations of spiders that do not routinely self-amputate their pedipalps (Chamberlin and Ivie, 1934; Knoflach and van Harten, 2000, 2001; Knoflach and Benjamin, 2003). There are several elegant studies that have examined the influence of pedipalp loss on sperm induction, and copulatory behavior but these studies did not explicitly quantify the influence of pedipalp loss on changes in pre-mating displays or test for lateralization effects of lost or impaired pedipalps (Rovner, 1966a,b, 1967; Rovner, 1971; Rovner and Wright, 1975).

Male *P. milvina* use the first pair of legs extensively during courtship displays (see Montgomery, 1903, and Kaston, 1936, for a complete description of *P. milvina* courtship), as do many species in the genus *Pardosa* (Koomans *et al.*, 1974). Pedipalps of male *P. milvina* are particularly conspicuous since they are covered by black setae that contrast sharply with the brown color of the legs and body. Additionally, males actively wave the pedipalps during courtship which suggests they may function as an active component of the male's visual display (Hebets and Uetz, 2000). Prior to formal courtship, the male rolls the medial surface of the pedipalp across the substrate when contacting silk embedded with sex pheromones from a virgin female (Rypstra *et al.*, 2003). Detection of the silk then initiates localized mate searching and low-intensity courtship until contact with the female is made. These observations suggest that pedipalps may also be important for chemical detection of females by male *P. milvina*.

There were two main objectives of our study. The first was a census of the frequency and pattern of pedipalp loss by age class and sex in the wolf spider *P. milvina*. We expected that adult male wolf spiders would have a higher incidence of pedipalp loss because of higher activity levels and conspicuousness relative to adult females and juveniles (Kotiaho *et al.*, 1998; Persons, 1999; Persons and Uetz, 1999; Walker *et al.*, 1999). Also, the frequency of leg loss is significantly higher among adult males than females and is also higher among juveniles (Brautigam and Persons, 2003). The second objective was to measure shifts in male courtship behavior and female response due to pedipalp loss. We tested if male wolf spiders missing one or both pedipalps reduced courtship intensity or otherwise compromised courtship displays. Recent studies indicate that *P. milvina* leg raise and body shake rates significantly influence mating success (Rypstra *et al.*, 2003; Brautigam and Persons, 2003) and is therefore used in female mate choice. If pedipalp waving has a species recognition function, we expected females to reject mating attempts by males missing one or both pedipalps more often than intact individuals and that females would respond slower to palp-autotomized males, as measured by longer courtship duration and increased latency to mount. Since pedipalps appear to have many chemosensory hairs used in pheromone detection of females (Tietjen and Rovner, 1982), the loss of one or more pedipalps may compromise the ability of the male to effectively locate females and therefore delay the onset of courtship and mating. If pedipalp-waving is an important part of a male wolf spider's courtship display, then males who are unable to perform this behavior should suffer lower mating success. We also expected an increase in cannibalism and aggression toward these males if pedipalp-waving is used as a species recognition cue.

METHODS

Field Census of Pedipalp Loss

Male ($N = 332$) and female ($N = 539$) *P. milvina* of various age classes were collected in corn and soybean fields in Snyder County, PA, from May to August, 2000. Each spider was transferred to the laboratory where they were individually maintained in 6 oz. plastic containers lined with moistened peat moss. Within 12 h of collecting, each spider was sexed and categorized by age class (adult females without egg sacs, adult females with egg sacs, subadult females, adult males, or subadult males). Juveniles too small for accurate sex determination were not collected. Individual spiders were then identified as missing none, one (right or left), or both pedipalps. Differences in pedipalp loss among categories were analyzed using a chi-square goodness-of-fit test.

Estimating the Courtship and Mating Costs of Pedipalp Loss

General Spider Collection and Maintenance

We tested the effects of male pedipalp loss on courtship, mating, and intersexual agonistic behavior. Intact subadult male and female *P. milvina* collected from the census data were used in this study as well as additional subadult individuals that were collected in corn and soybean fields (Susquehanna University, Selinsgrove, Snyder County, PA) from May to August 2000. Spiders were then individually reared until maturity in the lab to insure virginity of all adult spiders. Spiders were housed separately within 8-cm diameter × 5-cm high plastic translucent containers lined with moistened peat moss and maintained on a 13 L:11 D photoperiod at ambient room temperature (22–25°C). Each spider was fed once a week with a mixed diet of four to seven 5-day-old house crickets (*Acheta domesticus*) and several fruit flies (Canton-S strain, *Drosophila melanogaster*).

Hunger Standardization and Pedipalp Removal Procedure

To minimize variation in courtship, mating, and female aggressive and cannibalistic behavior attributable to hunger, we standardized hunger levels for all test spiders prior to mating. After maturation, unmated male and female spiders were given as many crickets as they could eat within a 24-h period. Excess food was then removed from each container and spiders were denied additional food for 6 days, approximating natural levels of hunger (Edgar, 1969; Nyffeler and Breene, 1990). Two days after feeding to satiety, each male spider was placed in a clean plastic container over ice for 30 s. This served to slow his movement and provide an anesthetic. Pedipalp autotomy was induced by pinching the designated pedipalp on the femur with a pair of entomological forceps causing the spider to subsequently self-amputate the limb along the coxa–trochanter joint (Johnson and Jakob, 1999; Brautigam and Persons, 2003). There were three induced autotomy treatments of virgin male *P. milvina* along with a control; individual males were randomly divided among treatments: (1) both pedipalps autotomized ($N = 33$), (2) left pedipalp autotomized ($N = 36$), (3) right pedipalp autotomized ($N = 34$), and (4) chilled, but no pedipalps autotomized ($N = 36$). Spiders in the control group underwent a sham operation by also being put on ice for 30 s followed by a light pressing of the femur with entomological forceps but not sufficiently to induce autotomization.

Pairing Procedure

Four days after the limb autotomy procedure, each experimental male was paired with a randomly selected unmated female. Prior to pairing, a set of 20-cm diameter round plastic containers was rinsed with ethanol to remove extraneous odors that might modify spider responses. A circular sheet of paper was then placed on the bottom of each container and fixed in place using masking tape. Tape was used to prevent spiders from crawling under the paper and out of view during videotaping. A female spider was then placed inside the container and given access to water via two 2.5-cm diameter vial lids placed on opposite sides of the sheet of paper. Females were left in the container overnight and allowed to deposit pheromone-laden silk draglines for 20 h. The following day, 4 days after male autotomization of pedipalps, the water lids were removed from the female's container and male and female spiders were allowed to interact. The male spider was introduced into the female's container under an inverted clear plastic 40-dram vial and allowed to acclimate for 5 min. The male spider was then released to freely interact with the female for 30 min or until the male mated and dismounted the female. All pairings were videotaped from above and analyzed later to reduce the possible effects of observer presence on spider behavior. Testing was conducted from 8:00 h to 18:00 h from late May through early August 2000. Trials for all treatments were randomized throughout the day and over subsequent days and weeks to control for possible time-of-day and sequence effects.

Behavioral Measurements

For each mating trial the following information was recorded: pedipalp-removal treatment, number of male leg raises, number of male body shakes, female lunges toward the male, cannibalism of males by females, time of courtship initiation by male since placed with the female (courtship latency), duration of time elapsed from the beginning of the trial to when the male mounted the female (mounting latency), and the total time the male was mounted on the female (mounting duration). We defined "mount" as the male climbing on the dorsum of the female prior to copulation. For purposes of this study, we defined copulation as an insertion of the pedipalp into the female epigynum. This distinction is used throughout since males that lack pedipalps cannot copulate, but can mount, which among intact males is nearly always followed by copulation and is considered a strong indicator of female acceptance and receptivity toward the male. Leg raises, pedipalp raises, and body shakes are components of the male mating display and have been described in detail elsewhere (see Montgomery, 1903; and Kaston, 1936). The anterior pair of legs is used in a visual display where the legs are simultaneous raised and lowered. Male spiders will usually raise their pedipalps in unison with leg raises but may also raise them independently of leg raises. The third component, body shakes, occurs when the spider's body vibrates rapidly for bouts lasting from 1–2 s. Leg raises and body shakes were both converted to rates by dividing total number of occurrences of that courtship element by the total courtship duration. Courtship duration was defined as the time from initiation of leg raises or body shakes until mounting occurred or until the 30-min trial period had expired.

Statistical Analyses

We used separate one-way ANOVAs and *post hoc* comparison of means (Tukey test) to analyze courtship latency, body shakes/s, leg raises/s, total courtship displays/s, mounting latency, mounting duration, and total number of lunges at the male by the female for each limb loss treatment. Courtship latency, mounting latency, and mounting or copulation duration were natural log transformed prior to analysis to conform to assumptions of normality. All other variables approximated normal distributions without transformation. We used chi-squared goodness-of-fit tests to compare mounting success and incidence of cannibalism across treatments.

RESULTS

Field Census of Pedipalp Loss

Missing pedipalps was relatively uncommon among field-collected spiders. Out of 871 *P. milvina*, 14 had one or both missing pedipalps, comprising only 1.6% of the population (Table I). We found significant differences in the pattern of pedipalp loss among the various age and sex classes of spider ($\chi^2 = 24.895$; $p < 0.0001$; Table I). Field-caught adult males were most likely to have a missing pedipalp, significantly more likely than adult females ($\chi^2 = 4.314$, $p = 0.0378$) but not subadult males ($\chi^2 = 2.7$, $p < 0.09$). Of the 14 spiders with missing pedipalps, 12 were adult males comprising 5% of the adult male population. The remaining two spiders with missing pedipalps consisted of one adult female and one subadult

Table I. Frequencies of Pedipalp Loss Among Age and Sex Classes of Field-Caught *Pardosa milvina* Wolf Spiders from May Through August 2000 ($N = 871$)

	Adult female	Adult female w/o egg sac	Subadult female	Subadult male	Adult male
Intact	126	165	247	91	228
Pedipalps missing	1	0	0	1	12
% missing pedipalps	0.8	0	0	1	5

male. Only one spider, a single adult male, had more than one pedipalp missing.

Courtship and Mating Costs of Pedipalp Loss

We found no significant difference in male mounting success across treatments ($\chi^2 = 2.33$, $p < 0.50$; Table II), nor did intact males spend significantly shorter amounts of time courting or mounted on the female than did pedipalp-autotomized males (Table III). However, males with the left or both pedipalps autotomized took a significantly longer time period to begin courting than either intact individuals or those that had their right pedipalp lost (Table III). In general, the loss of the left pedipalp had greater effects on courtship than the loss of the right. Courtship intensity varied significantly among pedipalp treatments (Table III). Individuals with the left or both pedipalps autotomized displayed significantly fewer leg raises than other treatments. There were also fewer body shakes completed among males with the left pedipalp lost compared to the right pedipalp or intact males (Table III).

A total of 10 adult male spiders were cannibalized across all pedipalp treatments (7.4%). Males with both pedipalps autotomized were significantly more likely to be cannibalized than other treatments ($\chi^2 = 8.58$, $p <$

Table II. Mounting of Females and Cannibalism of Males Across Pedipalp Removal Treatments

	Intact males ($N = 33$)	Left pedipalp removed ($N = 36$)	Right pedipalp removed ($N = 33$)	Both pedipalps removed ($N = 33$)
Mount	22 (67)	20 (56)	22 (67)	16 (48)
No mount	11 (33)	16 (44)	11 (33)	17 (52)
Cannibalized	0 (0)	2 (6)	2 (6)	6 (18)
Not cannibalized	33 (0)	34 (94)	31 (94)	27 (82)

Note. Percentage of all subjects within a treatment indicated in parentheses.

Table III. Courtship and Related Pre-Mating and Mounting Behaviors (Mean ± SE) Measured for Adult Male and Female *Pardosa milvina* by Pedipalp Removal Treatments

Behavior	Both pedipalps removed (33)	Left pedipalp removed (36)	Right pedipalp removed (33)	Intact males (33)	$F_{3,132}$	p
Number of female attacks/pairing	3.67 ± 0.78^{a}	3.25 ± 0.65^{a}	1.79 ± 0.34^{b}	1.46 ± 0.30^{c}	3.71	0.013*
Latency to court (s)	160.8 ± 44.3^{a}	162.9 ± 46.0^{ab}	85.1 ± 30.9^{bc}	45.12 ± 8.77^{c}	2.72	0.047*
Courtship duration (s)	831.7 ± 135.9	883.3 ± 116.3	516.0 ± 111.9	677.912 ± 134.3	1.79	0.153
Mount duration (s)	718.2 ± 125.8	766.9 ± 89.7	823.8 ± 115.7	1058.8 ± 120.1	1.73	0.167
Leg raises/min	0.206 ± 0.037^{a}	0.190 ± 0.023^{a}	0.284 ± 0.034^{b}	0.331 ± 0.043^{b}	3.87	0.011*
Body shakes/min	0.152 ± 0.034^{ab}	0.113 ± 0.017^{a}	0.208 ± 0.026^{b}	0.202 ± 0.028^{b}	3.10	0.029*

Note. Number of pairs used in each treatment is indicated in parentheses below each treatment. *F* ratio is based on one-way ANOVAs for each behavioral category. Letters superscripted above each mean indicate significant differences between treatments based on a Tukey *post hoc* comparison of means test. Behaviors without letters were not statistically significant at the 0.05 alpha level based on the omnibus test. Identical letters indicate groups that are not significantly different from each other.

0.036; Table II). Males with missing pedipalps were also significantly more likely to be attacked by females (Table III).

DISCUSSION

Field caught adult males of *Pardosa milvina* were significantly more likely to be missing a pedipalp than adult females and had the highest frequency of pedipalp loss of any age/sex class (Table I). Pedipalp loss was found in only 5% of the adult male population. However, we suggest that the true prevalence of pedipalp loss may be considerably higher. Ten percent of males with one or both pedipalps missing were cannibalized during encounters with virgin females. It is difficult to estimate male encounter rates with females, however *P. milvina* can occur at densities of over five individuals/m^2 (Marshall and Rypstra, 1999) and male *P. milvina* are highly mobile with males traveling an average of 431 cm in 30 min (Walker and Rypstra, 2003). Therefore, encounter rates with females are likely to be high and males with missing pedipalps are less likely to survive interactions with females, contributing to an underestimate of the actual rate of pedipalp loss. For the same reason, very low prevalence of males with two pedipalps missing may be underestimated since these males are cannibalized by virgin females in 18% of encounters.

It remains unclear why pedipalp loss was more prevalent in males than females or juveniles. Adult male *P. milvina* are not significantly more active than females (Walker and Rypstra, 2003); however, male courtship displays together with higher activity levels may render male wolf spiders more conspicuous and therefore susceptible to predators (Kotiaho *et al.*, 1998). Results of our study indicate that conspecific females may also be a significant source of male predation. Despite cannibalism and high levels of female aggression during trials, we observed no pedipalp or limb loss during male–female courtship and mating interactions suggesting that although it may be a significant source of mortality for pedipalp-autotomized males, it may not be a frequent direct cause of palp loss. Studies of the wolf spider *Schizocosa ocreata* found that leg loss occurred in 11% of all male–female pairings ($N = 135$) with the first pair of legs being lost significantly more often than other pairs (Persons and Uetz, 2005). However, as in our study, no incidences of pedipalp loss were observed during courtship interactions. Given the absence of observed pedipalp loss during male–female interactions in our study, the most likely reason for male-biased pedipalp loss may be failure of the pedipalp to be successfully extracted from the exuvia during the ultimate molt. Since male *P. milvina* pedipalps are larger and more developed among adult males than those in the penultimate instar, this likely creates a constriction around the old exuvia that makes extraction particularly difficult. This molting difficulty is likely unique to penultimate males but could potentially be a difficulty among antepenultimate instar males as well since these males also have enlarged pedipalps, albeit less so than penultimate individuals. Since our data show no significant difference in pedipalp loss between penultimate and adult males, this may be the case. If males do have the old exuvium trapped only around one or both pedipalps, autotomization may be the only viable option other than dragging it around with them through the environment where it likely would greatly hamper movement and feeding as well as interfere with courtship and increase predation risk.

We found that male pedipalp loss significantly reduced male courtship intensity (leg raise rates and body shake rates), but had no significant impact on mounting success or mounting duration. This was particularly surprising given that recent studies have found that courtship intensity in *P. milvina* is significantly associated with mating success (Brautigam and Persons, 2003; Rypstra *et al.*, 2003). Some detailed manipulative studies of several species of wolf spiders however have shown that males with plugged, restrained, or autotomized pedipalps are still capable of courtship displays, achieving mounts on the female, and engaging in copulatory or pseudocopulatory behavior (Rovner, 1966a,b, 1967; Rovner and Wright, 1975). Rovner and Wright (1975) suggested that pedipalp fatigue may be the proximate mechanism that terminates mating in the wolf spider *Schizocosa saltatrix* and *S. avida*. Although there was a nonsignificant trend toward shorter mounting duration among palpless males, time spent mounted did not vary among our treatments suggesting that mounting duration was largely determined by some other mechanism in *P. milvina* such as cessation of female abdomen rotation or increased female activity.

Unexpectedly, we found evidence of significant differences in courtship behavior depending on whether the left or right pedipalp was lost. Males missing the left pedipalp showed significantly reduced courtship latencies than intact males and less intense courtship (Table II). More importantly, females attacked males with the left pedipalp missing significantly more often than individuals with the right or no pedipalps missing. Quantitative studies on the morphological differences between the right and left pedipalp have not been done in lycosids. There has also been little work done comparing the role of the left and right pedipalp in sound generation, visual signaling during courtship, or chemoreception. As such, any causative explanation for differences between pedipalps must remain speculative. The visual components of the male's courtship display appear to be symmetrical with both pedipalps and the first pair of legs being raised in unison

(Montgomery, 1903). This suggests no real difference in visual information conveyed by the left or right pedipalp. However, some aspects of the courtship display occur so quickly that they may only be accurately analyzed with high-speed cinematography. Further, there have never been comparative measurements of density or distribution of decorative setae on each pedipalp. Critical differences in sound production by each pedipalp are also possible but largely unknown. We did note that the pedipalps appeared to contact the substratum during courtship, making sound production likely. Rovner (1967) experimentally removed one or both pedipalps of courting *Rabidosa rabida* wolf spiders and found that sound production was primarily through the pedipalps. Another possible explanation for the difference in male behavior and female response is asymmetry in the distribution of chemosensory hairs on the left and right pedipalp used to detect female sex-pheromones. Previous studies have demonstrated that the onset and intensity of *P. milvina* courtship is mediated largely by the detection of female pheromones (Searcy *et al.*, 1999; Rypstra *et al.*, 2003) and the pheromones, in turn, are detected primarily through the pedipalps (Tietjen and Rovner, 1982). Rypstra *et al.* (2003) showed that the absence of female pheromones reduced the number of leg shakes and body shakes during male courtship. Since body shake and courtship rates are used in the assessment of males by females (Brautigam and Persons, 2003; Rypstra *et al.*, 2003), then males with low courtship intensity may be valued more as a potential meal than a mate and result in increased aggression by females (Persons and Uetz, 2005). Regardless of the proximate mechanism generating these differences, our results strongly suggest some lateralization of use or asymmetry in some morphological aspect of male pedipalps that is critically important for species recognition by females or inhibiting aggression toward males.

Yoward and Oxford (1996) and Stratton *et al.* (1996) reviewed pedipalp usage patterns in all spiders and wolf spiders, respectively. Yoward and Oxford (1996) showed that some species of non-lycosid spider have biased pedipalp use and routinely use only a single pedipalp during mating, however in these studies there was no evidence of pedipalp lateralization at the species level. Although Stratton *et al.* (1996) found species specific variation in copulatory patterns among lycosids, all species apparently used both pedipalps during mating.

Given that pedipalp loss significantly affected cannibalism risk and female aggression levels but had no significant impact on mounting success, we suggest that pedipalps are not necessary to achieve a successful mount, but could function specifically in reducing female aggression. It remains unclear if pedipalp-waving in *P. milvina* is a visual display or merely a by-product of sound production or attempts to detect female pheromones and silk. Given the distinct pigmentation of the pedipalps relative to the rest of the body, coupled with the synchronization and pattern of the display, we suggest that pedipalp-waving is probably a visual display and may serve as an amplifier for a visual signal (Hebets and Uetz, 2000). Nonetheless, this signal is not crucial in female mate choice, but instead appears to be critical for reducing predatory behaviors in females.

ACKNOWLEDGMENTS

We thank Drew Hardick for help in collecting and maintaining spiders during this study. This research was funded by a grant from the Susquehanna University Research Partners Program and a Susquehanna University Faculty Research Grant. Additional support was provided by NSF grant C-RUI DBI 0216776 for M. Persons and C-RUI DBI 0216947 for A. Rypstra.

REFERENCES

Amaya, C. C., Klawinski, P. D., and Formanowicz, D. R. (2001). The effects of leg autotomy on running speed and foraging ability in two species of wolf spider (Lycosidae). *Am. Midl. Nat.* **145:** 201–220.

Brautigam, S. E., and Persons, M. H. (2003). The effect of limb loss on the courtship and mating behavior of the wolf spider *Pardosa milvina* (Araneae: Lycosidae). *J. Insect Behav.* **16:** 571–587.

Brueseke, M. A., Rypstra, A. L., Walker, S. E., and Persons, M. H. (2001). Leg autotomy in the wolf spider *Pardosa milvina:* A common phenomenon with few apparent costs. *Am. Midl. Nat.* **146:** 153–160.

Chamberlin, R. V., and Ivie, W. (1934). A new genus of theridiid spiders in which the male develops only one palp. *Bull. Univ. Utah* **24:** 2–18.

Edgar, W. D. (1969). Prey and predators of the wolf spider *Lycosa lugubris*. *J. Zool.* **159:** 405–411.

Hebets, E. A., and Uetz, G. W. (2000). Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). *Behav. Ecol. Sociobiol.* **47:** 280–286.

Johnson, S. A., and Jakob, E. M. (1999). Leg autotomy in a spider has minimal costs in competitive ability and development. *Anim. Behav.* **57:** 957–965.

Kaston, B. J. (1936). The senses involved in the courtship of some vagabond spiders. *Entomol. Am.* **16:** 97–167.

Klawinski, P. D., and Formanowicz, D. R. (1995). Ontogenetic change in survival value of leg autotomy in a wolf spider, *Gladicosa pulchra* (Keyserling) (Araneae: Lycosidae), during scorpion attacks. *Can. J. Zool.* **72:** 2133–2157.

Koomans, M. J., Van der Poleg, S. W. F., and Dijkstra, H. (1974). Leg wave behaviour of wolf spiders of the genus *Pardosa* (Lycosidae, Araneae). *Bull. Br. Arachnol. Soc.* **3:** 53–61.

Kotiaho, J., Alatalo, R. V., Mappes, J., Parri, S., and Rivero, A. (1998). Male mating success and risk of predation in a wolf spider: A balance between sexual and natural selection? *J. Anim. Ecol.* **67:** 287–291.

Knoflach, B., and Benjamin, S. P. (2003). Mating without sexual cannibalism in *Tidarren sisyphoides* (Araneae, Theridiidae). *J. Arachnol.* **31:** 445–448.

Knoflach, B., and van Harten, A. (2000). Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). *J. Nat. Hist.* **34:** 1639–1659.

Knoflach, B., and van Harten, A. (2001). *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behavior: Emasculation, male palpal organ as a mating plug and sexual cannibalism. *J. Zool. Lond*. **254:** 449–459.

Marshall, S. D., and Rypstra, A. L. (1999). Patterns in the distribution of two wolf spiders (Araneae: Lycosidae) in two soybean agroecosytems. *Environ. Entomol.* **28:** 1052–1059.

Montgomery, T. H. (1903). Studies on the habits of spiders, particularly those of the mating period. *Proc. Acad. Sci. Phil.* **4:** 59–149.

Nyffeler, M., and Breene, R. G. (1990). Evidence of low daily food consumption by wolf spiders in meadowland and comparison with other cursorial hunters. *J. Appl. Entomol.* **110:** 73–81.

Persons, M. H. (1999). Hunger effects on the foraging responses to perceptual cues in immature and adult wolf spiders (Lycosidae). *Anim. Behav*. **57:** 81–88.

Persons, M. H., and Uetz, G. W. (1999). Age and sex-based differences in the use of prey sensory cues in wolf spiders (Araneae: Lycosidae). *J. Insect Behav.* **12:** 723–736.

Persons, M. H., and Uetz, G. W. (2005). Sexual cannibalism and mate choice decisions in wolf spiders: Influence of male size and secondary sexual characters. *Anim. Behav.* **69:** 83–94.

Rovner, J. S. (1966a). Courtship in spiders without prior sperm induction. *Science* **152:** 543–544.

Rovner, J. S. (1966b). Copulation and sperm induction by normal and palpless male linyphiid spiders. *Science* **157:** 835.

Rovner, J. S. (1967). Acoustic communication in a lycosid spider (*Lycosa rabida* Walckenaer). *Anim. Behav*. **15:** 273–281.

Rovner, J. S. (1971). Mechanisms controlling copulatory behavior in wolf spiders (Araneae: Lycosidae). *Psyche* **78:** 150–165.

Rovner, J. S., and Wright, E. E. (1975). Copulation in spiders: Experimental evidence for fatigue effects and bilateral control of palpal insertions. *Anim. Behav*. **23:** 233–236.

Rypstra, A. L., Wieg, C., Walker, S. E., and Persons, M. H. (2003). Mutual mate assessment in wolf spiders: Differences in the cues used by males and females. *Ethology* **109:** 297–306.

Searcy, L. E., Rypstra, A. L., and Persons, M. H. (1999). Airborne chemical communication in the wolf spider *Pardosa milvina* (Araneae, Lycosidae). *J. Chem. Ecol.* **25:** 2527–2533.

Stratton, G. E., Hebets, E. A., Miller, P. R., and Miller, G. L. (1996). Pattern and duration of copulation in wolf spiders (Araneae, Lycosidae). *J. Arachnol*. **24:** 186–200.

Tietjen, W. J., and Rovner, J. S. (1982). Chemical communication in lycosids and other spiders. In Witt, P. N., and Rovner, J. S. (eds.), *Spider Communication: Mechanisms and Ecological Significance*, Princeton University Press, Princeton, NJ, pp. 249–280.

Uetz, G. W., McClintock, W. J., Miller, D., Smith, E. I., and Cook, K. K. (1996). Limb regeneration and subsequent asymmetry in a male secondary sexual character influences sexual selection in wolf spiders. *Behav. Ecol. Sociobiol*. **38:** 253–257.

Walker, S. E., Marshall, S. D., Rypstra, A. L., and Taylor, D. H. (1999). The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). *Anim. Behav.* **58:** 515–520.

Walker, S. E., and Rypstra, A. L. (2003). Sexual dimorphism and the differential mortality model: Is behaviour related to survival? *Biol. J. Linn. Soc.* **78:** 97–103.

Yoward, P., and Oxford, G. (1996). Single palp usage during copulation in spiders. *Newsl. Br. Arachnol. Soc*. **77:** 8–9.