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Leg Autotomy in the Wolf Spider Pardosa milvina: A Common Phenomenon with Few Apparent Costs

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ABSTRACT.—A number of animals escape predation by sacrificing a body part. Spiders commonly lose legs in encounters with predators or conspecifics. We investigated the frequency of leg loss and its affect on locomotion and prey capture activities of the wolf spider, *Pardosa milvina* (Araneae; Lycosidae). In addition, we determined if *Pardosa* were easier to subdue by the larger wolf spider predator, *Hogna helluo* (Araneae; Lycosidae), once they had experienced leg loss. A field census demonstrated that *Pardosa* autotomized members of all pairs of legs with equal frequency but overall leg loss was high and increased significantly late in the season. Laboratory experiments revealed that leg loss had no effect on locomotory behavior or prey capture. However, injured spiders tended to take smaller prey. The ability of *Hogna,* to attack and subdue 7 or 8-legged *Pardosa* was not different, although 8-legged *Pardosa* tended to lose multiple legs as they were killed whereas 7-legged *Pardosa* only lost one. These data suggest that the costs of autotomizing one leg are marginal for *Pardosa* females and, thus, support the ''spare leg hypothesis'' that has been proposed for other arachnids.

INTRODUCTION

Many animals risk being injured or killed during aggressive interactions with other organisms. If an animal survives an agonistic encounter with an injury, it may not be able to perform critical activities and, ultimately, is less able to survive and reproduce. However, there are a number of species that sacrifice a leg or tail in an encounter in order to escape more easily (Lawrence *et al.*, 1986; Arnold, 1994; Juanes and Smith, 1995; Johnson and Jakob, 1999). Such self-amputation or autotomy is an effective way to escape predators that grasp body parts during an attack (Lawton, 1989; Formanowicz, 1990; Arnold, 1994; Klawinski and Formanowicz, 1994). However, once the body part is lost, the injured animal may experience decreased foraging success, decreased reproductive success, reduced competitive ability and/or changes in growth patterns (Riechert, 1988; Buck and Edwards, 1990; Spivak, 1990; Cheng and Chang, 1993; Dodson and Beck, 1993; Arnold, 1994; Juanes and Smith, 1995, Uetz *et al.*, 1996).

Many species of spider autotomize legs during interactions with aggressive conspecifics or predators (Formanowicz, 1990; Klawinski and Formanowicz, 1994; Punzo, 1997). Field collections of a variety of species reveal that between 5 and 40% of individuals in natural populations are missing one or more legs (Dodson and Beck, 1993; Foelix, 1996; Punzo, 1997; Johnson and Jakob, 1999). However, only a handful of studies have investigated the costs of leg loss for spiders and the results seem to depend on the spider species examined and the particular life history feature investigated (Riechert, 1988; Dodson and Beck, 1993; Johnson and Jakob, 1999; Amaya *et al.*, 2001). It might be expected that leg loss would be particularly problematic for wolf spiders (Lycosidae) because most species do not use webs

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and, thus, the legs are very important in foraging and locomotion (Rovner, 1980). Nevertheless, wolf spiders autotomize legs readily in encounters with predators or aggressive conspecifics (Formanowicz, 1990; Klawinski and Formanowicz, 1994; Punzo, 1997) and, after such a traumatic event, will avoid substratum previously occupied by the predator that inflicted the damage (Punzo, 1997). The removal of a leg resulted in lower sprint speeds in two species of wolf spider and, therefore, may affect their ability to escape a predator (Amaya *et al.*, 2001). Additionally, in the largest members of one of those same species, the loss of a leg also made prey capture more difficult (Amaya *et al.*, 2001).

Here we report the results of a comprehensive study of leg loss in a small and very active species of wolf spider, *Pardosa milvina* (Hentz) (Araneae: Lycosidae). The goals of this study were: (1) to estimate the frequency with which leg loss occurred in natural populations; (2) to quantify the effects of leg loss on locomotor activities and prey capture efficiency; and (3) to determine if, after losing a leg, individuals were more easily captured by a predator.

STUDY SPECIES

The wolf spider *Pardosa milvina* (hereafter referred to as *Pardosa*) dominates the vagrant spider population of agricultural habitats in North America (Young and Edwards, 1990) and is particularly common at the Miami University Ecology Research Center (Marshall and Rypstra, 1999). *Pardosa* is a small spider (20 mg) that subdues other arthropods by overwhelming them with its chelicerae and legs before it bites and kills with venom (Rovner, 1980). In our regular field collections leg loss was relatively common with some individuals missing as many as six legs. Since this species is an active forager (Walker *et al.*, 1999) and a common prey item for other spiders in the environment (Persons and Rypstra, 2000), we attempted to quantify how the loss of a leg affected its activity levels, prey capture behaviors and ability to escape predation.

METHODS

Field census.—In order to determine the frequency of leg loss in a natural population, we collected *Pardosa* regularly from 28 May through 20 August 1999 at Miami University's Ecology Research Center located 3 mile N or Oxford, Butler County, Ohio. Spiders were collected in and adjacent to the agricultural fields described in Marshall and Rypstra (1999). For each individual we recorded the number and position of missing legs. The frequency and distribution of leg loss was compared across the season using chi-squared tests.

Laboratory manipulations.—All spiders used in laboratory experiments were females collected with a full complement of eight legs at Miami University's Ecology Research Center. In the laboratory they were housed individually in plastic containers (7.5 cm diam) with 2 cm of sphagnum peat moss covering the bottom. Spiders were provided with water ad lib. and fed prey at least twice weekly (crickets—*Acheta domesticus* or fruit flies—*Drosophila melanogaster*). Before and during experimentation, all animals were held in an environmental chamber maintained at 25 C on a 14:10 L:D cycle. Before experimental removal of a leg, *Pardosa* females were anesthetized by chilling. We then grasped one of the first pair of legs with forceps at the joint between the coxa and trochanter and gently pulled until it was free. Control spiders were chilled and held in a similar manner. In all cases, there was at least a 24 h recovery time before testing.

Locomotor behavior.—We tested the effect of the loss of one of the first pair of legs on the activity of adult female *Pardosa*. The spiders were fed one cricket the day before the experiment and only used in the following test if the prey was consumed. In each run a single spider was placed in a cylindrical plastic container (20 cm diam) with white filter paper covering the bottom. After a 15 min acclimation period, the spider's activity was monitored remotely for an additional 15 min using a Videomex-V automated behavioral monitoring system as in Walker *et al.* (1999). Spider location was recorded every second and the activities were summed every 3 min interval for the 15 min session. Between sessions, containers were swabbed with 95% ethanol, allowed to air dry completely and the filter paper was replaced. A total of 15 intact (8-legged) and 15 injured (7-legged) spiders were tested. We tested the predictions that leg loss would reduce activity by comparing the time spent moving, average speed over the entire 15 min period and the total distance traveled in the 15 min session as well as the maximum speed recorded (fastest speed in any 3 min interval) between groups using one-tailed *t*-tests.

Prey capture.—This experiment was designed to test the effect of the loss of one of this first pair of legs on *Pardosa* foraging behavior. The spiders were fed small cricket nymphs (*Acheta domesticus*) ad lib. 1 d before testing. Only those adult female spiders that consumed prey were used in this test in order to ensure consistent hunger levels across treatments. After this feeding, one of the first pair of legs was removed from the experimental group. One day later each spider was placed in a cylindrical plastic container (8 cm diam). A single cricket nymph, approximately 25% the size of the spider, was weighed and then placed in the center of this container under a translucent plastic vial (1 cm diam). Both animals were allowed 5 min to acclimate. At that time the vial was lifted and the interactions between the spider and the cricket were observed for 15 min or until the spider began to eat the cricket. Containers were swabbed with 95% ethanol and allowed to dry completely between trials. A total of 15 intact and 15 injured spiders were used. We tested the prediction that leg loss would compromise foraging behavior by comparing the time to subdue prey, and the size of the crickets captured between 7 and 8-legged spiders using one-tailed *t*-tests. In addition, we compared the total number of attempts at predation (lunges) made by spiders in the two groups using the Mann-Whitney test.

Predator avoidance.—In this experiment we tested the effect of the loss of one of the first pair of legs on the ability of a female *Pardosa* to escape predation. The predator used was *Hogna helluo* Walkenaer (Araneae; Lycosidae), a large spider that coexists with and readily preys upon *Pardosa* in our study areas (Marshall and Rypstra, 1999; Persons and Rypstra, 2000). Both spider species were collected and maintained individually in the laboratory under the conditions described above. One wk before testing all spiders were provided with crickets ad lib. for 24 h. They were then held with water but no food for 7 d before experimentation. A single *Hogna* was placed in a plastic container (20 cm diam) and allowed 60 min to acclimate. A *Pardosa* was then introduced under a translucent vial (1 cm diam) into the center of the arena and allowed to acclimate for 5 min. After the acclimation time, the vial was lifted and the spiders were observed for 30 min or until the *Hogna* began to consume the *Pardosa*. A total of 41 intact and 41 injured *Pardosa* were tested. Containers were wiped clean with 95% ethanol and allowed to dry completely between any trials. The frequency of predation and the frequency with which legs were lost during interactions were compared between groups using chi-squared tests. We tested the prediction that the loss of a leg would render a spider more susceptible to predation by comparing the total time it took for *Hogna* to subdue 7 or 8-legged *Pardosa* using a one-tailed *t*-test.

RESULTS

Field census.—Across the season 104 of 635 spiders collected were missing legs. Thus, 16.4% of this population were missing at least one leg. In order to look for seasonal differences in leg loss we divided our collections into three time periods, each containing approximately the same number of spiders. The early period extended from 28 May

TABLE 1.—Frequency with which leg loss was observed in field collections of *Pardosa milvina* during 1999. The percentages listed for the total number of spiders missing legs are the number in that category out of all collected in that time period. The percentages listed for the frequency with which a particular leg was missing are the number of spiders who had lost a member of that pair out of all the spiders in that time period with legs missing. There was a seasonal effect on leg loss ($\chi^2 = 22.15$, df = 2, $P < 0.001$). There was no particular pair of legs that was more likely to be lost than others ($\chi^2 = 22.15$, df = 2, $P < 0.001$). There was no particular pair of legs that was more likely to be lost than others ($\chi^2 = 1.54$, df = 3, $P = 0.62$)

Season	Number censused	Total missing one leg %	Total missing 2 or more legs %	Total missing legs %	Leg 1 lost %	Leg 2 lost %	Leg 3 lost %	Leg 4 lost %
Early	217	15	3	18	6	2	6	8
		6.9%	1.3%	8.3%	27.3%	9.1%	27.3%	36.4%
Middle	214	17	2	19	5	5	4	7
		7.9%	0.9%	8.9%	23.8%	23.8%	19.0%	33.3%
Late	204	47	20	67	23	24	21	23
		23.0%	9.8%	32.8%	25.3%	26.1%	23.1%	25.3%
Total	635	79	25	104	34	31	31	38
		12.4%	3.9%	16.4%	25.4%	23.1%	23.1%	28.4%

through 8 July, the middle period extended from 9 July through 8 August and the late period extended from 9 August through 20 August 1999. The frequency of leg loss was significantly different among periods with much higher frequency of leg loss in August collections ($\chi^2 = 22.15$, df = 2, $P < 0.001$) (Table 1). There were 79 cases of spiders missing one leg, 21 cases of spiders missing two legs and 4 cases of spiders missing three legs. Leg loss was evenly distributed among the four pairs of legs in *Pardosa* (Table 1) ($\chi^2 = 1.54$, df = 3, $P = 0.62$).

Locomotor behavior.—No significant differences were evident between intact and injured spiders in the total distance traveled, the total time spent in motion, the average speed at which they moved during the 15 min test run (Table 2). Similarly, the maximum speed we

TABLE 2.—Behavioral characteristics (mean ± SE) measured for *Pardosa* with one of the first pair of legs experimentally removed as compared to *Pardosa* with a full complement of eight legs. In all cases the critical values provided are for one-tailed *t*-tests performed to test the hypotheses that injured spiders would not perform as well as intact spiders except for the number of lunges where a Mann-Whitney test was performed and the estimate of z is provided

Characteristic	8-legged spider	n	7-legged spider	n	*t* (*z)	P
Total distance traveled (cm)	262.5 ± 43.8	15	214.3 ± 34.9	15	−0.861	0.397
Time in motion (s)	11.1 ± 0.8	15	11.4 ± 1.6	15	0.133	0.896
Average speed (cm/s)	2.0 ± 1.5	15	1.8 ± 0.2	15	−0.702	0.489
Maximum speed (cm/s)	3.0 ± 0.3	15	2.6 ± 0.3	15	−0.964	0.344
Weight of crickets provided (mg)	5.5 ± 0.4	15	5.1 ± 0.4	15	0.775	0.223
Weight of crickets consumed (mg)	5.6 ± 0.4	13	4.6 ± 0.3	13	1.936	0.032
Time to subdue cricket (s)	1.5 ± 1.5	13	2.0 ± 1.4	13	−0.839	0.410
Time for *Hogna* to subdue *Pardosa* (s)	932.5 ± 99.8	29	807.6 ± 119.6	33	−0.789	0.433
Number of lunges at cricket	1.1 ± 0.3	15	1.3 ± 0.5	15	−0.809*	0.419

TABLE 3.—The number of 7 and 8-legged *Pardosa* killed by the predator, *Hogna*, during trials with information as to whether legs were lost in the interaction or not. Intact *Pardosa* were more likely to lose multiple legs in an interaction with a predator than injured *Pardosa* ($\chi^2 = 3.96$, df = 1, P = 0.04)

	7-legged *Pardosa*		8-legged *Pardosa*	
	Killed by *Hogna*	Survived	Killed by *Hogna*	Survived
No legs lost	22	8	20	12
One leg lost	10	1	6	0
2 or more legs lost	0	0	3	0
Total	32	9	29	12

recorded in any 3 min interval during the test was not significantly different between the two groups (Table 2).

Prey capture.—A total of 13 of the 15 *Pardosa* in each of the treatment groups captured a cricket. Although the weights of the crickets we provided both groups of *Pardosa* were not significantly different, the crickets captured by spiders with one of leg experimentally removed were smaller than the crickets captured by spiders with all 8 legs (Table 2). There were no significant differences between injured and intact *Pardosa* in the number of times they lunged at the cricket during attack (Table 2) or in the total time it took to subdue their prey (Table 2).

Predator avoidance.—The predator, *Hogna,* consumed 33 of the 41 (80.5%) *Pardosa* missing a front leg and 29 of the 41 (70.7%) *Pardosa* with all eight legs. The likelihood of a *Pardosa* surviving a predator attack in this experiment was not different between groups ($\chi^2 = 0.746$, df = 1, P = 0.388) (Table 3). One injured *Pardosa* lost an additional leg in the interaction with the *Hogna* and survived (Table 3). None of the survivors in the control group lost a leg in the interaction with *Hogna*. In about a third of the trials with both treatment and control groups, *Hogna* removed one or more legs before killing the *Pardosa* (Table 3). When *Pardosa* lost legs in the process of being attacked and killed by the *Hogna, Pardosa* with 8 legs at the outset were more likely to lose two or three legs than 7-legged *Pardosa*. At most, 7-legged *Pardosa* lost one additional leg while they were attacked and killed by a *Hogna* (Table 3). The total time it took *Hogna* to subdue and kill *Pardosa* was not significantly different between treatment groups (Table 2).

DISCUSSION

Leg autotomy is a frequent occurrence in our population of *Pardosa milvina*. In August 1999 32% of the animals we collected were missing legs which is well above the range typically reported for spiders (5–20%; Foelix, 1996) (however, Dodson and Beck (1993) found that in populations of crab spiders, male–male conflict resulted in higher levels of leg loss). Although some of the missing legs may have been lost during molting (Foelix, 1996), the high rate of leg loss we observed in *Pardosa* suggests that encounters with potential predators were fairly frequent in our population. Our laboratory experiments revealed few costs to female *Pardosa* in executing day-to-day activities, whereas the benefit of losing a leg, if it means surviving a predator attack, would be extremely high. Thus, sacrificing a leg may be an important advantage for *Pardosa* in avoiding predation.

Our population had a much higher frequency of leg loss in August than in earlier months in the same year (Table 1). The entire community of spiders, including *Pardosa,* in the habitats under study increases across the summer to a peak in the late summer and early fall (Rypstra and Carter, 1995; Marshall and Rypstra, 1999). Since spiders are major predators of other spiders and other predatory arthropods (Hodge, 1999), the increased density undoubtedly resulted in more encounters with other spiders, more opportunities for predation attempts and, therefore, resulted in more instances of leg autotomy. In addition, 1999 was a very dry year in Ohio and spiders may have tended to congregate in areas where moisture and cover were available. If so, such high localized densities could force the animals into more encounters with one another and lead to a higher rate of leg loss.

Our survey collections revealed that *Pardosa* did not tend to autotomize a member of any particular pair of legs (Table 1). In our experiments we focused on the effects of removal of one of the first pair of legs on adult females because previous studies of wolf spiders suggested that the anterior legs were lost most often (Uetz *et al.*, 1996). Characteristics of the first pair of legs, including their symmetry, are important in the courtship behaviors performed by male wolf spiders and ultimately selection by the female (Uetz *et al.*, 1996). Thus, males would more likely experience a more direct reduction in fitness due to leg autotomy than females. Since the focus of this study was to address the effects of autotomy on the nonreproductive activities of movement, prey capture and predator escape, we limited our investigation to females who, except when a male is present and courting, are very active (Walker *et al.*, 1999).

Basic parameters of locomotion we measured were unaffected by the loss of a front leg (Table 2). In contrast, Amaya *et al.* (2001) found that the loss of a leg significantly reduced sprint speed in two other wolf spider species. The spiders they tested were larger (25–700 mg) and the speeds they recorded were much faster (40–55 cm/s) than those we recorded for *Pardosa,* so the biomechanics of locomotion would be substantially different among these species. Guffey (1999) argued that arachnids are capable of compensating for the loss of one or two legs with only minor adjustments. Spiders employ an alternating walking pattern and, when a leg is lost, they change the stride length and the position of the remaining legs to close up the gap left by the missing leg (Foelix, 1996). Spiders that lose one leg or two on opposite sides of the body are still capable of smooth locomotion using a system of alternating tripods (Wilson, 1967).

In prey capture, wolf spiders tend to approach and grab the prey with the legs and chelicerae, and then insert the fangs to inject venom (Rovner, 1980). It is not uncommon to see the predator and prey roll on their dorsal side as they grapple with their prey (pers. obs.). In our prey capture experiment we observed no difference in the attack behavior of intact or injured *Pardosa* (Table 2). However, intact spiders tended to consume larger crickets than those with one of the first pair of legs removed (Table 2). Likewise, Amaya *et al.* (2001) found that leg loss affected prey capture in the largest examples of one of the two species they tested. Taken together, these results suggest that leg loss may have a negative impact on prey capture at certain ratios of spider to prey size. If, indeed, 7-legged *Pardosa* take smaller prey than 8-legged spiders, this difference could have direct fitness effects for female spiders. If autotomy results in a female passing up a large prey item at a critical time, it may directly reduce the size of the egg sac produced and/or the number of eggs it contains and thus directly reduce reproductive success.

Most studies of autotomy in relation to predators have focused on its efficacy in enabling the animal to escape the predator (Formanowicz, 1990; Klawinski and Formanowicz, 1994; Punzo, 1997). However, the question we attempted to address in our predator tests was whether the loss of a leg enhanced the ability of a predator to capture the spider. Thus, our design gave *Pardosa* little opportunity to escape if the *Hogna* predator was motivated to consume it. Indeed, similar numbers of *Pardosa* were killed in each treatment group (Table 3). More germane to our question, however, is the fact that *Hogna* performed the same number of lunges in the same amount of time in the process of subduing 7 or 8-

legged *Pardosa*. This result suggests that leg loss did not render *Pardosa* more vulnerable, except, of course, because they had fewer legs to sacrifice. In their interaction with *Hogna* some injured *Pardosa* lost legs, but none of them lost more than one additional appendage (Table 3). On the other hand, several 8-legged *Pardosa* lost two or three legs as *Hogna* was subduing them (Table 3). If the loss of each leg actually translated into an opportunity to escape, then intact *Pardosa* may have had a survival advantage over injured *Pardosa* because they had more legs to give up.

We tested several hypotheses that leg loss compromised the daily activities of *Pardosa* and found little evidence of significant costs to leg autotomy. Although we observed a relatively high frequency of leg loss in the field, cases of multiple leg loss were rare and only 6 of the 635 spiders we censused had lost more then 2 legs. Similarly, when we tested the effects of leg loss on susceptibility to predation, our injured spiders only gave up one additional leg whereas intact spiders frequently autotomized several legs. These results are consistent with the ''spare leg hypothesis'' proposed by Guffey (1998, 1999) for harvestmen. He argues that some arachnids have more legs than they actually require for daily activities and so they can afford to sacrifice one of them with minimal cost (Guffey, 1998, 1999). Female *Pardosa* may have a sufficient number of legs such that the loss of one of them does not compromise their ability to function in the environment and thus does not cause any substantial reduction in expected fitness (Guffey, 1998, 1999). In order to test this hypothesis critically, one would have to test the effects of multiple vs. single leg loss and map any detectable costs on reproductive success in a direct manner.

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LITERATURE CITED

AMAYA, C. C., P. D. KLAWINSKI AND D. R. FORMANOWICZ. 2001. The effects of leg autotomy on running speed and foraging ability in two species of wolf spider (Lycosidae). *Am. Midl. Nat.,* **145**:201–205.

ARNOLD, E. N. 1994. Caudal autotomy as a defense, p. 235–273. *In:* C. Gans and R. B. Huey (eds.). Biology of the reptilia 16, Ecology B: Defense and life history. Alan R. Liss, New York, N.Y.

BUCK, C. AND J. S. EDWARDS. 1990. The effect of appendage and scale loss on instar duration in adult firebrats, *Thermobia domestica* (Thysanura). *J. Exp. Biol.,* **151**:341–347.

CHENG, J.-H. AND E. S. CHANG. 1993. Determinants of postmolt size in the American Lobster (*Homarus americanus*). I. D_1^3 is the critical stage. *Can. J. Fish. Aq. Sci.,* **50**:2106–2111.

DODSON, G. N. AND M. W. BECK. 1993. Pre-copulatory guarding of penultimate females by male crab spiders, *Misumenoides formosipes. Anim. Behav.,* **45**:289–299.

FOELIX, R. F. 1996 The biology of spiders, 2nd ed. Oxford University Press, Oxford. 306 p.

FORMANOWICZ, D. R., JR. 1990. The anti-predator efficacy of spider leg autotomy. *Anim. Behav.,* **40**: 400–401.

GUFFEY, C. 1998. Leg autotomy and its potential fitness costs for two species of harvestmen (Arachnida, Opiliones). *J. Arachnol.,* **26**:296–302.

———. 1999. Costs associated with leg autotomy in the harvestmen *Leiobunum nigripes* and *Leiobunum vittatum* (Arachnida: Opiliones). *Can. J. Zool.,* **77**:824–830.

HODGE, M. A. 1999. The implications of intraguild predation for the role of spiders in biological control. *J. Arachnol.,* **27**:351–362.

JOHNSON, S. A. AND E. M. JAKOB. 1999. Leg autotomy in a spider has minimal costs in competitive ability and development. *Anim. Behav.,* **57**:957–965.

JUANES, F. AND L. D. SMITH. 1995. The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *J. Exp. Marine Biol. Ecol.,* **193**:197–233.

KLAWINSKI, P. D. AND D. R. FORMANOWICZ, JR. 1994. Ontogenetic change in survival value of leg autotomy in a wolf spider, *Gladicosa pulchra* (Kesyerling) (Araneae: Lycosidae), during scorpion attacks. *Can. J. Zool.,* **72**:2133–2135.

LAWRENCE, J. M., T. S. KLINGER, J. B. MCCLINTOCK, S. A. WATTS, C.-P. CHEN, A. MARSH AND L. SMITH. 1986. Allocation of nutrient resources to body components by regenerating *Luidia clathrata* (Say) (Echinodermata: Asteroidea). *J. Exp. Marine Biol. Ecol.,* **102**:47–53.

LAWTON, P. 1989. Predatory interaction between the brachyuran crab *Cancer pagurus* and decapod crustacean prey. *Marine Ecol. Progress Ser.,* **52**:169–179.

MARSHALL, S. D. AND A. L. RYPSTRA. 1999. Habitat selection determines the colonization of two soybean agroecosystems by two wolf spiders (Araneae: Lycosidae). *Environ. Ent.,* **28**:1052–1059.

PERSONS, M. H. AND A. L. RYPSTRA. 2000. Preference for chemical cues associated with recent prey in the wolf spider *Hogna helluo* (Araneae: Lycosidae). *Ethology,* **106**:27–35.

PUNZO, F. 1997. Leg autotomy and avoidance behavior in response to a predator in the wolf spider, *Schizocosa avida* (Araneae; Lycosidae). *J. Arachnol.,* **25**:202–205.

RIECHERT, S. E. 1988. The energetic cost of fighting. *Am. Zool.,* **28**:877–884.

ROVNER, J. 1980. Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). *J. Arachnol.,* **8**:201–215.

RYPSTRA, A. L. AND P. E. CARTER. 1995. The web-spider community of soybean agroecosystems in Southwestern Ohio. *J. Arachnol.,* **23**:135–144.

SPIVAK, E. D. 1990. Limb regeneration in a common South American littoral crab Cyrtograppsus angulatus. *J. Nat. Hist.,* **24**:393–402.

UETZ, G. W., W. J. MCCLINTOCK, D. MILLER, E. I. SMITH AND K. K. COOK. 1996. Limb regeneration and subsequent asymmetry in a male secondary sexual character influences sexual selection in wolf spiders. *Behav. Ecol. Sociobiol.,* **38**:321–326.

WALKER, S. E., S. D. MARSHALL AND A. L. RYPSTRA. 1999. The effects of hunger on locomotory behaviour in two species of wolf spider (Araneae, Lycosidae). *Anim Behav.,* **58**:515–520.

WILSON, D. M. 1967. Stepping patterns in tarantula spiders. *J. Exp. Biol.,* **47**:133–151.

YOUNG, O. P. AND G. B. EDWARDS. 1990. Spiders in United States field crops and their potential effect on crop pests. *J. Arachnol.,* **18**:1–27.

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