

**MORPHOLOGICAL AND ETHOLOGICAL ADAPTATIONS  
FOR PREY CAPTURE IN WOLF SPIDERS  
(ARANEAE, LYCOSIDAE)<sup>1</sup>**

**Jerome S. Rovner**

Department of Zoology  
Ohio University  
Athens, Ohio 45701

**ABSTRACT**

High-speed cinematography and experimental modification of morphological features were used to study the adaptations of lycosid spiders for capturing large, dangerous prey. Removal of the scopula hairs from the legs (by shaving) reduced the spider's ability to restrain crickets from escape. Observations suggested the importance for prey capture of other features of the legs: (1) a primarily flexor musculature for grasping strength; (2) an efficient hydraulic mechanism for rapid extension; (3) erectile spines for protection from the prey; and (4) relatively great length, permitting manipulation of prey at a safe distance from the body. Captures involving "de-fanged" spiders indicated that the chelicerae alone are sufficient for prey retention, neither fangs nor legs being needed during cheliceral grasping. Captures involving spiders prevented from using their chelicerae and fangs suggested that the venom apparatus is essential only for immobilization of already-restrained large prey so that ingestion can begin. Descriptive data point to prey capture being a family-specific behavior; consequently, there has evolved a diversity of guilds within the wandering spiders.

**INTRODUCTION**

The ability of wandering spiders to overpower relatively large prey involves several heretofore little-studied structural and behavioral adaptations. Some specializations make up for the lack of a silk trap, which aids web-weavers by interrupting the prey's locomotion and by restraining it from escape during subsequent handling. Another specialization, the venom apparatus, is present in all wandering spiders and most web-weaving spiders; however, its role has not been examined with regard to its relative importance in the overall predatory sequence. The present study includes the first experimental investigation of the roles of these various morphological adaptations in prey capture by wandering spiders.

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By means of high-speed cinematography, I was able to examine the predatory behavior of several species of *Lycosa*. Much of this behavior resembled that of the ctenid *Cupiennius salei* (Keyserling) studied by Melchers (1967). Based on Melchers' and my data, I developed hypotheses about the functions of various appendage adaptations; then I observed the behavior of experimentally modified spiders to test these hypotheses. Significant roles were indicated for the adhesive scopula hairs and the erectile spines on the legs. In addition, support was provided for Anderson and Prestwich's (1975) hypothesis that the preponderance of flexor muscles in the legs of spiders improves prey-holding ability, and Enders' (1975) hypothesis that the venom apparatus evolved in spiders to enable them to utilize large prey and thereby obtain more food per capture than would a non-venomous predator of similar size. Finally, the concept of a "guild of wandering spiders" was questioned in light of ideas generated in the present study, as was Enders' (1975) hypothesis that webs evolved in spiders as tools for subduing larger prey than nonweb spiders can handle.

## METHODS

Most observations were made on adult female *Lycosa rabida* Walckenaer, *L. aspersa* Hentz, and *L. helluo* Walckenaer. Subjects were deprived of their maintenance feeding of mealworms (*Tenebrio molitor* L.) for one week and then filmed during the capture of adult domestic crickets (*Acheta domesticus* L.). The spiders had a body length of  $18.2 \pm 1.48$  mm ( $n=10$ ); the crickets,  $23.8 \pm 1.87$  mm ( $n=10$ ), or about 30% longer than the spiders. Most of the spiders weighed 400-600 mg; the crickets, 600-1000 mg. Smaller spiders were offered smaller crickets within the size range; larger spiders, larger crickets. In most of the predatory sequences filmed, the prey were larger and heavier than the spiders.

For each film session I placed a spider into an all-glass arena, 100 mm in height, whose back wall was covered with paper to prevent reflection of light into the camera. The arena floor measured 80 mm front-to-back, 100 mm wide, and was covered with paper to provide traction. The arena's dimensions provided adequate room for interactions like that shown in Fig. 10, while yielding a film image with sufficient magnification and depth-of-field for later analysis. Each filming sequence was initiated when a cricket that had climbed out of a vial, which rested on the arena ceiling, fell through a hole into the arena. (In early attempts to film, I waited until the spider began to pounce before starting the camera and thereby missed part of the interaction.)

A Cine-8 Super-8 mm camera (Visual Instrumentation Corp., Burbank, California) (Model SP-1) and a Kinoptik 50 mm  $f/2$  Macro-Apochromat lens were used. The camera was kept in a fixed position on the tripod. A pair of 500-W slide projectors, one on each side of the front of the arena, provided illumination. Using Kodak 4-X reversal film (ASA 400) and a lens setting of  $f/11$ , I was able to obtain sufficiently bright and sharp images at the maximum camera speed of 250 fps. Films were analyzed on a Kodak Ektagraphic projector (Model MFS-8). A total of 207 prey capture attempts on 36 reels of film were examined (176 of *L. rabida*, 20 of *L. aspersa*, and 11 of *L. helluo*). In addition, photographs were taken with the aid of two, synchronized, electronic flash lamps (Rollei E15B; flash duration =  $1/2000$  sec). Species photographed included the above three, as well as *L. punctulata* Hentz and *L. timuqua* Wallace. (As in the few *L. aspersa* studied, the individuals of *L. timuqua* were about as large as the crickets.)

To prevent experimental spiders from envenomating the prey, I applied melted paraffin to the flexed fangs of anesthetized ( $\text{CO}_2$ ) spiders and sealed the fangs into the cheliceral grooves. (This was performed on three *L. rabida*.) When I also wished to prevent use of the chelicerae, these appendages were bound together with a distally placed cast of paraffin (Fig. 1). Three *L. rabida*, one *L. aspersa*, and one *L. helluo* received this combined treatment. Spiders so treated did not starve; each could still use its endites and labium to feed by scavenging on cut-up mealworms that I placed in their home cages.

Another type of experimental modification involved removal of the scopula hairs from the ventral and lateral surfaces of the tarsi and metatarsi of all the legs, and from the tibiae of the anterior two pairs. For each such operation I anesthetized the spider, inverted it, and "stapled" its body and legs to a styrofoam block with pairs of pins. Then, while observing it under a stereomicroscope, I shaved off the scopulae with a microscalpel. During the 2-3 hr of shaving, the spider occasionally struggled briefly to free itself, not being under anesthesia. The spiders subjected to this modification were those five that previously had been treated to prevent envenomation and use of the chelicerae; therefore, they had been filmed capturing prey prior to being shaved. Thus, the same individuals provided data for both the unshaven and the shaven conditions.

In analyzing the effect of scopula removal, I compared the unshaven vs. the shaven conditions on the basis of the number of prey escapes per total bouts of contact by the spiders. A 2X2 contingency table (Model I), using the *G*-statistic (Sokal and Rohlf 1969), served to test  $H_0$ : prey retention is independent of the presence of scopula hairs on the legs. Throughout this paper, means are accompanied by S.D.'s.

## RESULTS

### I. Control spiders

**Orientation Toward the Prey.**—The spiders turned to face (and then approached) the prey in response to visual or vibratory cues. Spiders sometimes could respond visually to leaping crickets arcing above them by rapidly re-orienting to the moving target and capturing the insect as it landed. In response to vibrations induced by a cricket walking behind it, the spider performed one or more pivoting movements to face the prey.

In some cases the spider performed a sudden "pivot leap" to partly or completely face a cricket that had just landed behind it. This began with a synchronous spine erection on all of the spider's legs; the spider then twisted and raised the anterior end of its body as it lifted the anterior three pairs of legs. It twisted further and pushed with legs IV, the impetus of its pivot carrying the spider in a turn with all the legs now in the air, until a landing on the anterior three pairs of legs.

**The Pounce.**—Female *Lycosa* spp. could leap short distances to capture prey, such leaps covering about 1.5-2 body lengths of the spider. However, contact of legs IV with the substratum was lost for only about one body length, the leg IV tarsi sliding on the substratum for up to one-half of the leap, especially during the landing. In most captures the pounce was a response to prey within reach and did not involve such a true leap into the air; i.e., the leg IV tarsi maintained contact with the substratum throughout the pounce. The pounce in this case involved a push forward and obliquely upward, with the partly flexed legs I already raised into a high arch (and then legs II likewise); all of this resulted in lifting the spider's body to a position above the adjacent prey (Fig. 2).

In both types of pounces, while legs III sometimes may have contributed to the thrust, most of the propulsion was provided by legs IV. The activation of the hydraulic system needed to power the extension of these legs was reflected in the occurrence of synchronous spine erection in all the legs just prior to and throughout the pounce. Spine erection was first seen as legs I were raised (the first element of the pounce), which involved flexure of the trochantero-femoral and femoro-patellar joints. During the propulsive thrust, increased traction on the arena floor probably was provided by specialized scopula hairs on the plantar surfaces of legs III and IV (Type B leg scopula hairs, Rovner 1978).

**Contact and Restraint.**—Initial contact with the prey involved the distal ventral surface of the spider's legs I and II. After making contact, the spider pulled itself closer to the prey, an action requiring a firm hold by these anterior legs. With large prey, such as these crickets, legs III and then IV also were brought into contact, the eight legs forming a kind of "basket" that partly or completely surrounded the prey (Fig. 3).

Legs I and II continued to be the most important ones during the next portion of prey capture, since they served to position the spider's anterior end, thereby enabling the spider to bring its fangs into contact with the prey. The degree to which the less-used legs III and the least-used legs IV were employed depended on the activity level of the prey. Thus, in a struggle with a vigorously responding cricket, these posterior legs also were used both to restrain and to manipulate the prey; with less active prey, they were not used.

Since the cricket often kicked or pushed against the spider with its metathoracic legs, the loss of grip by one or more of the spider's legs was compensated for by the continued or renewed contact of its other legs. Even though the cricket often successfully thrust against the spider's sternum, abdomen, or proximal leg segments and thereby pushed the spider to a distance of a fully extended metathoracic leg, the spider did not lose contact with the prey. The spider was able to keep its tarsi (and perhaps metatarsi) pressed against the prey, the spider's legs being longer than the cricket's (Figs. 4 and 5).



Fig. 1.—Female *Lycosa punctulata* treated to illustrate the author's method of employing a paraffin cast (arrow) to prevent spiders from using their chelicerae and fangs.

**Orientation on the Prey and Fang Insertion Sites.**—During prey restraint, the spider typically had its body axis parallel to that of the cricket, spider venter against cricket dorsum. Since contact usually occurred as the cricket was moving away from the spider in an escape attempt, both animals faced in the same direction during capture in 88% of the cases (Fig. 6). To attain the final capture position, the spider pulled itself forward until its anterior end was near the cricket's thorax. Of the 51 captures in which both predator and prey faced the same direction, 26 fang insertion sites were in the thoracic region, 22 in the anterior abdomen, and 3 in the metathoracic leg (proximal segments). Of the 7 captures in which predator and prey were facing in opposite directions, 5 fang insertion sites were in the thoracic region, 2 in the anterior abdomen. Fang insertion sites in the thoracic and abdominal regions involved roughly equal proportions of dorsal, lateral, and ventral locations.

**Inversion.**—In preliminary trials on female *L. rabida*, 7 of 15 captures ended with the pair of animals inverted (Fig. 7). The inverted position was maintained for several minutes until the prey was immobilized by the venom. Then the spider regained an upright position by rolling to one side or forward while maintaining its cheliceral grip on the cricket.

That the inversion usually was due to the cricket's behavior was determined by observing the capture of crickets from which I had removed metathoracic legs. Only 3 of 15 captures involving crickets that lacked one leg ended in the inverted position. None of 20 captures involving crickets that lacked both metathoracic legs ended in the inverted position. During subsequent cinematographic studies, there were a few cases in which a capture ended in an inversion that was not caused by the metathoracic legs. Because of the basket-shaped configuration of the spider's legs when grasping large prey, a rolling of the spider (with its prey) resulted from the momentum of the pounce.

**Metathoracic Legs of the Cricket.**—Frame-by-frame analysis of prey capture behavior revealed the cricket's use of its jumping legs. These long, powerful appendages could be rotated at the base to aim in most directions in both the horizontal and vertical planes.

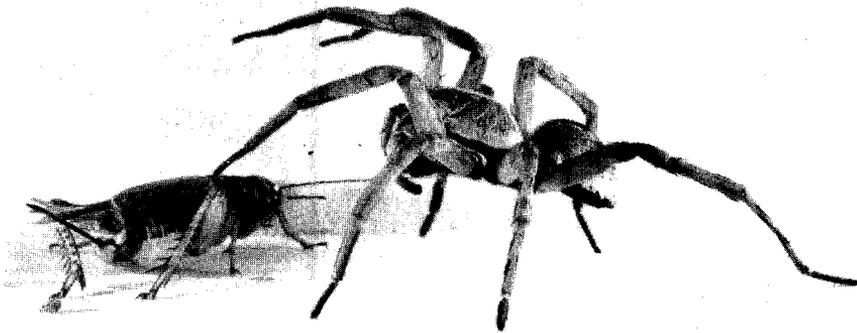


Fig. 2.—Female *Lycosa timuqua* about to pounce on a cricket (*Acheta domesticus*). Three of the spider's four anterior legs are raised.

They often were used in a directed manner, being aimed—even anteriorly—toward the spider during wrestling. The spines on the cricket's metathoracic legs sometimes engaged the spines on the legs of the spider, thereby improving the effectiveness of the thrust. Typically the cricket extended both legs synchronously, unless the movement of one of them was restricted by the spider.

When the spider was above the cricket and the cricket was upright, the latter's metathoracic leg thrusting against the substratum propelled both animals into a semi-elliptical trajectory through the air. In six filmed examples that could be measured, the pair of animals reached a height (taken as the distance from the spider's eyes to the substratum) of  $37 \pm 8.2$  mm, the highest being 48 mm (about 2.7 body lengths of the spider). These "flights" lasted  $0.15 \pm 0.03$  sec, as timed from the loss of contact with the substratum to renewed contact (Figs. 8, 9, and 10).

A series of several, synchronous, metathoracic leg thrusts sometimes occurred while the animals sailed through the air. The components of each thrust were executed very rapidly; e.g., from the fully extended position back to the maximally flexed position took only about 0.02 sec. Leg thrusts occasionally were effective in dislodging one or more of the spider's legs or in pushing the spider's body away, thereby temporarily loosening the grasp (Fig. 10g). The spider responded instantly to such actions by renewing contact of its just-dislodged legs or initiating a re-positioning of its body, i.e., a change in its orientation on the cricket. All of this occurred in flight while the spider clung to the prey. Rarely did these spiders lose total contact with the prey due to the latter's actions. Thus, the pair of wrestling animals traveled the entire trajectory as a unit.

**Contact Surface of the Spider's Legs.**—Throughout all of the above-stated events, the spider used its distal leg surfaces for contacting the prey. (The palps were not used in prey capture.) Thus, rather than tightly enclosing the prey and pressing against it with the entire ventral surface of its legs, the spider used the scopula-covered portions of the legs and often kept its body at a distance from the struggling cricket until fang insertion was attempted. The scopula hairs were erect during capture.

Two aspects of prey capture revealed in the films indicated the firmness of the plantar surface's grip: (1) Spiders were able to use one of their tarsi to hold onto the cricket's thrusting metathoracic leg; contact was maintained without slipping on the rapidly shifting substratum provided by the jumping leg. (2) Spiders could pull themselves forward and regain a position juxtaposed to the prey after the cricket had partially escaped from the spider's grasp. During mid-air interactions, after the cricket had leaped, the spiders were able to pull themselves upward onto the cricket from a position in which they had been hanging from the cricket.

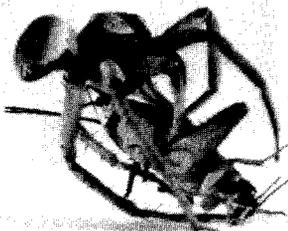


Fig. 3.—Female *Lycosa timuqua* enclosing a struggling cricket in a "basket" of legs. Note the spider's use of the distal leg segments for contact. (Exposure=1/2000 sec).

Film analyses showed a very minor role for the tarsal claws in prey restraint. Occasionally during a struggle, the claws on one or two of the spider's legs would engage joints or spines on the cricket's legs, thereby restricting movement of the latter to some degree.

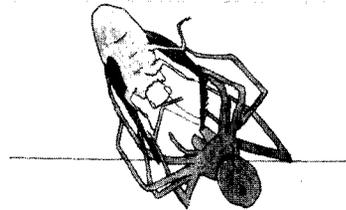
**Events After Fang Insertion.**—Soon after the spider succeeded in inserting its fangs and grasping the prey in its chelicerae, the spider removed most or all of its legs from contact, especially if in the inverted position. If above the prey or leaning back behind it, the spider extended legs I and II away from the prey. Contact by the legs was renewed briefly only to manipulate the prey or to restrain additional movements that preceded immobilization.

Even after envenomation had occurred, a lack of restraint of the prey prior to immobilization could result in its loss; consequently, the cheliceral grasp was maintained for a number of minutes until struggling ceased. Thus, feeding on large prey could begin only after the venom had immobilized it. In some cases, post-immobilization prey wrapping (Rovner and Knost 1974) also occurred prior to ingestion.

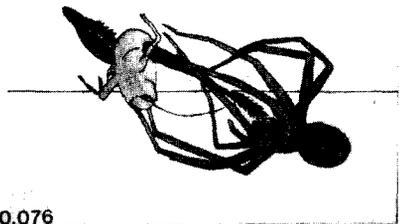
*II. Experimental Spiders*

**Modified Fangs.**—Spiders deprived of the use of their fangs (by having them sealed into the cheliceral grooves) still were capable of using their chelicerae to hold the cricket firmly. These muscular, toothed appendages were pressed together into the prey's body and provided a secure hold sufficient for restraint of a jumping cricket, without the need for continued leg contact by the spider. Such "de-fanged" spiders wrestled with the prey for over 1 hr, being unable to immobilize the prey in order to begin feeding. Every time that the cheliceral grip was relaxed, the cricket began to escape and had to be restrained once more, first with the spider's legs and then with its chelicerae.

**Modified Chelicerae.**—Spiders unable to use their chelicerae (due to a paraffin cast) had to maintain leg contact at all times in order to restrain the prey. Thus, such spiders'



0.000



0.076

Fig. 4.—Diagrams based on a film (recorded at 250 fps) of a female *Lycosa rabida* manipulating a struggling cricket. Although the cricket pushed its right metathoracic leg against the spider's sternum (lower diagram), the spider's longer legs enabled it to maintain contact with the prey and subsequently pull it back to a more proximate position. Elapsed time (sec) is at the lower left.

behavior was unlike that of untreated animals or of those with modified fangs, both of which extend their legs away from struggling prey as soon as a firm cheliceral grasp is achieved.

**Shaven Spiders.**—Removal of scopula hairs from the legs reduced but did not altogether eliminate the ability of the spiders to restrain crickets. The attempt to grasp the prey after making initial contact with legs I and II sometimes failed, especially if the cricket leaped in response. This may have been due in part to the tarsi slipping on the substratum during the approach (especially the leg IV tarsi that provide the thrust for the pounce), as revealed in the films. However, it was evident in many cases that the plantar surfaces of legs I and II had been pressed against the prey but slipped over the surface of the body rather than maintain a firm contact. In other cases, shaven spiders succeeded in at least establishing a temporary leg basket around the prey.

Although shaven spiders often could hang onto crickets during leaps by enclosing them in a leg basket, they were less able than unshaven ones to maintain control of struggling prey throughout the trajectory, especially if the cricket's metathoracic legs pushed against the spider. Thus, leg thrusting by the prey more often resulted in escape from shaven spiders than from unshaven ones. The data indicated a significant dependence ( $G = 39.474$ ;  $P < 0.001$ ) of the ability to restrain prey on the presence of leg scopula hairs. Shaven spiders lost the prey in 78 cases, more than twice as many times as they retained it (35 cases); while control spiders retained prey in 69 cases, nearly three times as often as they lost it (24 cases).

#### DISCUSSION

Data collected in this study indicate that the morphology of lycosid spiders reflects various adaptations that function in prey capture. Some of these specializations—adhesive hairs, a preponderance of flexor muscles in the legs, and leg length—also serve locomotor



Fig. 5.—Female *Lycosa rabida* inverted on the substratum and using the tips of its fully extended legs to manipulate a struggling cricket that was thrusting its metathoracic legs against the spider. (Photograph of a frame of Super 8 mm film exposed at 250 fps).

needs. Others—powerful chelicerae, a venom apparatus, and erectile spines—evolved specifically for predatory interactions. While lycosids were the subjects used here, many of the hypotheses discussed below are applicable to members of most families of wandering spiders.

**Adhesive Hairs.**—A locomotor role for the leg scopula hairs had been hypothesized by Homann (1957) and supported by Foelix and Chu-Wang (1975). A predatory function for these hairs (in addition to the locomotor one) was hypothesized by Rovner (1978), based on a survey of their distribution on the legs of diverse wandering spiders and their absence in web-weavers. The experimental approach in the present study has yielded support for both hypothesized functions. Shaven spiders tended to slip more than non-shaven ones as they attempted to move quickly over the substratum during prey capture. Likewise, shaven spiders showed a reduced ability to restrain prey from escape. Unfortunately, the experiment is confounded by the loss of sensory hairs due to shaving; their absence may have altered the ability of the spider to monitor pressure applied to a substratum.

The finding that unshaven spiders could restrain large crickets for prolonged periods by use of the distal leg surfaces alone, i.e., without the aid of chelicerae or fangs when so treated, provided further support for the hypothesized role of the adhesive hairs in predation. On the other hand, the ability to restrain prey was not eliminated entirely by shaving off the leg scopulae, indicating that these structures are not essential for this function. Thus, as with many morphological adaptations in animals, the adhesive hairs improve the effectiveness of a system but are not indispensable for some degree of success.

Acquisition and manipulation of the prey by the spider depended primarily on the anterior two pairs of legs. Effective traction was important for a successful landing on the cricket during a pounce, the initial contact being a critical point in the capture sequence. Subsequent restraint and manipulation of large prey usually involved the distal plantar surfaces of all four pairs of legs, the exclusive sites of the adhesive hairs. It is possible that the evolution of these hairs in wandering spiders related mostly to their role during predation on large or powerful prey, particularly those that could escape by leaping or flying. The natural prey of various lycosids, for example, includes grasshoppers, crickets, and other orthopterans, as well as adult lepidopterans and dipterans (Kuenzler 1958; Whitcomb and Bell 1964; Edgar 1969). Correspondingly, the jumping and flying abilities of the ancestors of such insects probably were, in part, evolutionary responses to predation by ancestral wandering spiders. Thus, we may have here a crude example of coevolution in a predator-prey relationship.

Fig. 6.—Female *Lycosa timuqua* attempting to restrain an escaping cricket just after the capture sequence was initiated. Note that both animals face in the same direction. The spider subsequently pulled itself forward to the typical, more anterior location in which its "leg basket" enclosed the prey. (Exposure=1/2000 sec).



**Leg Flexor Muscles.**—Closely associated with the localized gripping function of the adhesive hairs is the overall grasping ability of the spider imparted by the predominance of flexor muscles in the legs. The importance of this feature of spiders for prey capture was suggested by Anderson and Prestwich (1975). In the present study, the ability of unshaven spiders to restrain struggling crickets with the tips of the spider's fully extended legs (Figs. 4 and 5), and the ability of shaven spiders to partly restrain struggling crickets without the aid of the chelicerae or fangs, both provide evidence for the Anderson and Prestwich hypothesis: the spider's peculiar muscle arrangement—legs packed with flexors—is an adaptation yielding maximum grasping strength for prey capture.

**Hydraulic System.**—Shifting to a preponderance of flexors for prey capture meant having a dearth of extensors, which Anderson and Prestwich (1975) hypothesized led to the need for a hydraulic mechanism to provide for efficient leg extension. The importance of this feature was seen in two aspects of prey capture: (1) The propulsive force of the spider's leap or pounce depended mostly on the sudden extension of legs IV, a lesser version of that action described for a salticid spider by Parry and Brown (1959). The great increase in hydrostatic pressure just prior to the leap was indicated by the synchronous erection of the leg spines. (2) Spine erection continued throughout the time that the legs were used for grasping during the prey's struggling. The maintained high level of hydrostatic pressure enabled the spider to extend the legs rapidly, an important ability because of the need to move the legs away from the powerful kicks of the cricket's spiny metathoracic legs. Rapid leg extension also occurred during manipulation of a struggling prey, the leg first being lifted away and then placed at another site on the prey. Thus, during prey capture, high levels of activation of both the leg flexor muscles and the hydraulic mechanism for leg extension are occurring.

**Erectile Spines.**—Throughout most of the lycosid spider's life, the large spines rest against the leg surface, thereby not interfering with locomotion of the animal through narrow spaces in the physical structure of the environment, as would permanently erect spines. When the spines are erected, they probably make it difficult for an opponent to get close enough to the leg surface to injure the spider. In turn, the now spiny legs can be used to keep the opponent safely away from the spider's body. Only twice in all of the filmed encounters did a cricket succeed in biting the spider, in both cases on a distal leg segment. (In response, the spider immediately released the prey from its grasp.)

This view of a defensive function for the erectile spines supports the original hypothesis of Gaubert (1892) but disagrees with that recently proposed by Harris and Mill (1977). The latter workers regard these spines as "haemocoelic pressure monitors" and suggest that any defensive role is secondary "since the danger inflicted by an erecting spine would be minimal." However, Harris and Mill themselves point out that the spines

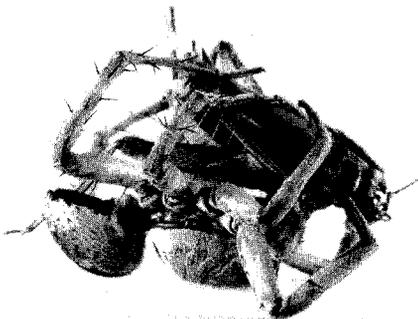


Fig. 7.—Female *Lycosa timuqua* lying inverted on the substratum after capturing a cricket.

are much larger than they need be for a receptor function. Furthermore, erection is maintained throughout two dangerous activities—prey capture and fighting with conspecifics (Rovner 1968). Finally, many spiders (e.g., oxyopids) only have permanently erect large spines (Gertsch 1949), yet presumably also must monitor hydrostatic pressure. Thus, I regard the erectile spines as defensive structures, whose receptor units provide information about the rate and degree of erection. Such information therefore can be monitored independently of other hydraulically mediated actions, such as erection of the adhesive scopula hairs (Rovner 1978), which accompanies spine erection during capture.

**Leg Length.**—While locomotor needs provide an important selective pressure in the evolution of leg morphology in wandering spiders, observations in the present study suggest that predatory needs play a part as well. Just as specialized leg lengths have evolved in certain spiders (e.g., thomisids) for particular methods of capture, the range of suitable leg lengths in the more generalized forms (e.g., lycosids) may be influenced by the need to combine grasping strength with the ability to keep the body at a safe distance from the weapons of dangerous prey.

**Chelicerae.**—Lycosids prevented from using their fangs still were able to restrain crickets by holding them with the chelicerae, even without the spider using the legs, once a firm cheliceral grip had been established. Thus, at some point in capture, these dentate appendages take over the function of restraint from the legs, which then are extended away from the prey and thereby removed from potential danger. Of course, in untreated spiders the fangs are driven into the prey's body by the chelicerae and provide additional aid in gripping the prey. Indeed, the fangs of spiders may have evolved from tooth-like precursors that served only for gripping in some non-venomous ancestral form.

**Venom Apparatus.**—While the chelicerae alone enabled the spider to restrain large prey, they did not suffice for the utilization of such prey, since ingestion required prey immobilization. Spiders experimentally prevented from using their fangs were unable to

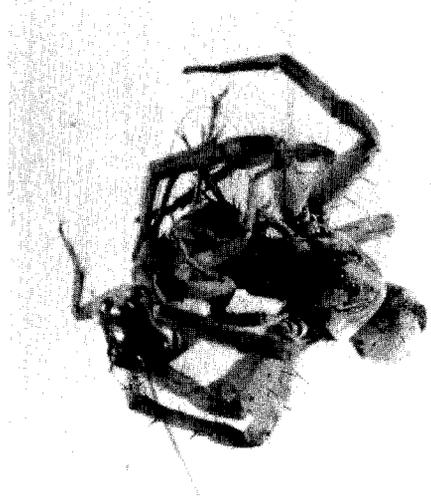


Fig. 8.—Female *Lycosa timuqua* wrestling with a cricket as both travel in a trajectory. The pair were catapulted upward by the cricket's metathoracic legs thrusting against the substratum. (Exposure=1/2000 sec).

begin feeding on large prey. Thus, for "de-fanged" spiders, capturing prey was not equivalent to acquiring a meal; the prey merely was held in check.

Enders (1975) had pointed out the lack of any experimental study that "demonstrates by how much a venom increases the upper limit of size of prey that is taken." The technique developed for the present study—sealing the fangs or the chelicerae—furnishes a suitable approach to this problem. Able to use the chelicerae but not the fangs, spiders can capture but not feed upon large prey. Thus, the venom apparatus does increase the upper limit of prey size taken, in that it enables the spider to begin ingestion. (For small prey, the chelicerae alone are sufficient for immobilization.) A quantitative answer to Enders' question of the size increase of the prey that venom provides for the spider would require presenting an array of prey sizes and types; nevertheless, the qualitative finding of my study does support his hypothesis. Thus, it is likely that the advantage of greater prey biomass per capture was the factor that produced the selective pressure for the evolution of the venom apparatus in spiders.

**Prey Morphology.**—While many caterpillars, flies, and other prey of lycosid spiders present no hazard, the cricket is potentially dangerous. Riechert (1973) reported that similar prey (locustid orthopterans) could use their metathoracic legs to perforate the soft integument of agelenid spiders when struggling took place in the confines of the funnel. While no such injuries occurred in the relatively open arena use in the present study, it is likely that capture attempts beneath objects or within the interstices of dense plant material near the ground would involve a similar danger to lycosids. Much (perhaps most) of the selective pressure for the evolution of the spines and musculature of these orthopterans' metathoracic legs probably came from predation by spiders.

**Prey Size.**—The prey used in my study usually were as large or larger than the spiders; furthermore, the prey were not defenseless. This refutes the assertion by Enders (1975)

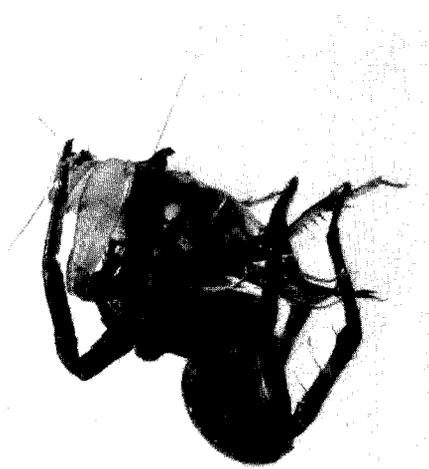


Fig. 9.—Female *Lycosa aspersa* using its distal leg segments to hang onto a cricket as both travel in a trajectory initiated by the cricket. (Exposure=1/2000 sec).

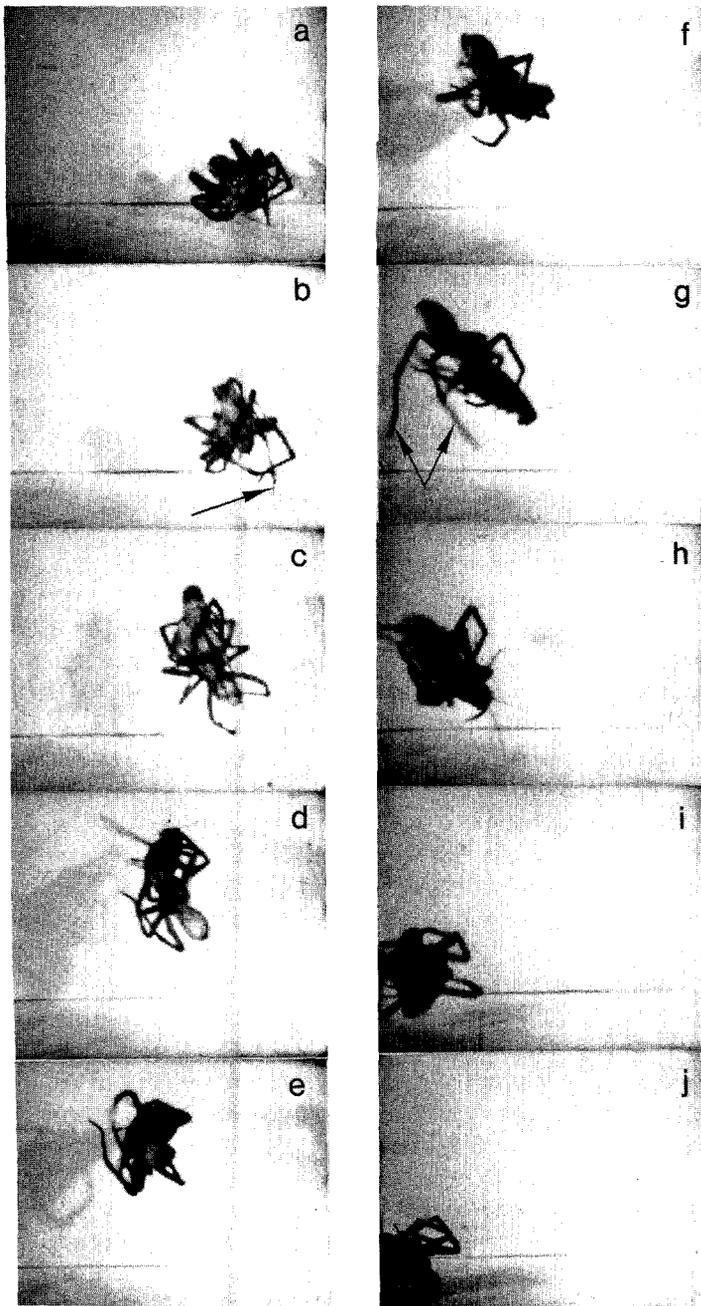


Fig. 10.—Female *Lycosa rabida* travelling in a trajectory with a struggling cricket, as recorded on Super 8 mm film at 250 fps. Every fifth frame of the film is shown; thus, the interval between pictures is 0.02 sec. The total sequence lasted 0.18 sec. In a-c the cricket's left metathoracic leg (arrow) thrusts against the substratum and lifts both animals obliquely upward. During d-f the zenith is reached (about 35 mm above the substratum), as the animals roll to a position with the spider above the cricket. In g the cricket's metathoracic legs thrust outward, dislodging the spider's right legs III and IV (arrows). In h the spider has returned these legs to contact with the prey. Impact with the substratum occurs in j.

that "terrestrial temperate-zone nonweb spiders of greater body weight (Lycosidae) are not reported to capture large prey." Enders was seeking to support his hypothesis that "the use of silk by the web spider is demonstrably the use of a tool or net to subdue larger (or more difficult) prey than the nonweb spider can handle." Observations herein, as well as those of Robinson and Valerio (1977) on salticids and of Whitcomb et al. (1966) on oxyopids, indicate that nonweb spiders readily capture large and often dangerous prey. Thus, Enders' hypothesis that webs arose as tools to increase the upper limit of size of prey is in doubt.

**Family-specific Capture Behavior.**—Patterns common to most of the interactions that were filmed suggested that there is a "lycosid style" of capturing large, dangerous prey. The pounce, while over a shorter distance than that of a salticid or oxyopid spider, likely gives lycosids a greater range of effectiveness than those wandering spiders that do not pounce. After contacting the prey, repeated re-positioning to avoid defensive weapons may represent a tactic that certain other wanderers (e.g., thomisids) do not include in their repertoire. The aggregate of behavioral elements available to each kind of spider for predation probably influences the success of capturing certain types of prey and, in turn, delineates this aspect of the spider's niche. While this aspect has been well-studied in web weavers, the wandering spiders have received little attention.

Studies of heteropodid and oxyopid spiders (Rovner, unpubl. data) likewise reveal predatory behavior that is probably characteristic for the family or perhaps even a lower taxon. While lycosids (Edgar 1969; Ford 1978), heteropodids, and oxyopids (Whitcomb and Bell 1964) are usually "sit-and-wait" predators, how and where the spider "sits," as well as how it contacts, restrains, and manipulates the prey, are different among the families. It is likely that the differences affect the kinds of prey captured. This brings into question the concept of a single "guild of wandering spiders" that some authors (e.g., Uetz 1977) have used in lumping these diverse spiders into a category implying a similar manner of resource exploitation. It seems more appropriate to follow Enders' (1975) viewpoint: Within each of the three major modes of hunting (which were originally suggested by Gertsch 1949)—short-sighted wanderers, long-sighted wanderers, and web spiders—there exist a number of guilds characterized on the basis of both hunting manner and prey type used. Indeed, one wonders if Post and Riechert's (1977) division of the wandering spiders of Tennessee forests and fields into only four guilds—diurnal runners, nocturnal runners, crab, and jumping spiders—represents a sufficient separation of wanderers comparable to the seven guilds of web dwellers that these authors appropriately distinguish. Future research may support the idea of several guilds, each definable in part by a unique combination of behavioral elements that constitute the predatory repertoire, within each of the present diurnal and nocturnal runner categories.

**Complexity of the Nervous System.**—The cinematographic analyses of Melchers (1967) and of the present study suggest another aspect of the predatory behavior of various wandering spiders—their extraordinarily rapid and complex responses to the prey's actions. (Melchers' finely tuned analysis includes data on the speed and complexity of predatory elements in the ctenid *Cupiennius salei*.) Compared to these spiders, the well-studied behavior of the mantis is simple—"aim and shoot." Unlike the latter insect, lycosid spiders must make many varied responses using most or all of their appendages during a brief interaction to secure the prey. This requires a nervous system that can make rapid analyses of an ever-changing stimulus situation in order to yield output that provides for continued control of the struggling prey while simultaneously adjusting the spider's position to reduce the possibility of injury from the prey's weapons.

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Fig. 1.—Female *Lycosa punctulata* treated to illustrate the author's method of employing a paraffin cast (arrow) to prevent spiders from using their chelicerae and fangs.

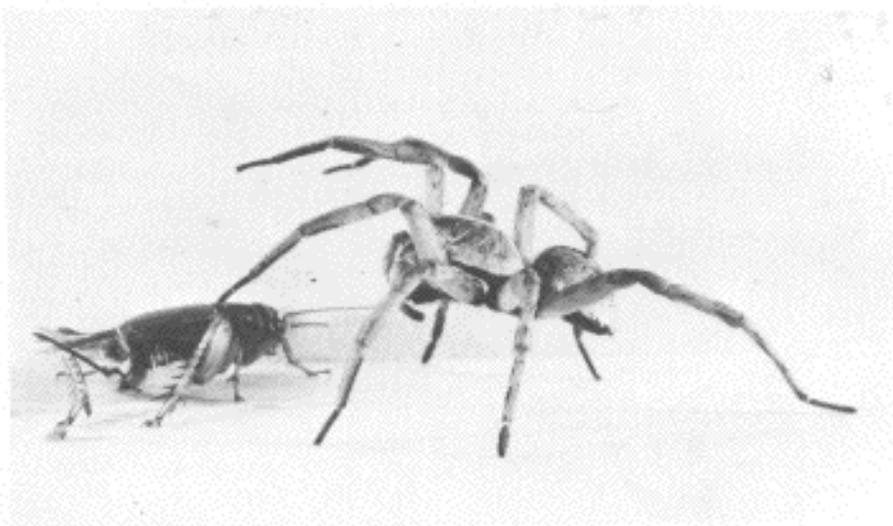


Fig. 2.—Female *Lycosa tinnuca* about to pounce on a cricket (*Acheta domestica*). Three of the spider's four anterior legs are raised.

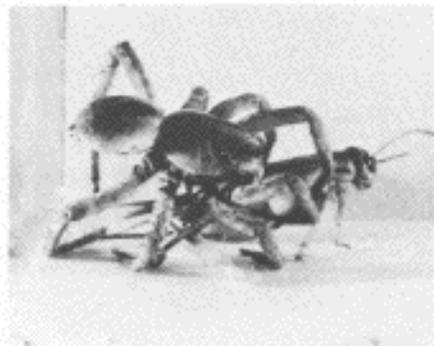


Fig. 3.—Female *Lycosa timuqua* enclosing a struggling cricket in a "basket" of legs. Note the spider's use of the distal leg segments for contact. (Exposure=1/2000 sec).



Fig. 5.—Female *Lycosa rabida* inverted on the substratum and using the tips of its fully extended legs to manipulate a struggling cricket that was thrusting its metathoracic legs against the spider. (Photograph of a frame of Super 8 mm film exposed at 250 fps).

Fig. 6.—Female *Lycosa timuqua* attempting to restrain an escaping cricket just after the capture sequence was initiated. Note that both animals face in the same direction. The spider subsequently pulled itself forward to the typical, more anterior location in which its "leg basket" enclosed the prey. (Exposure=1/2000 sec).



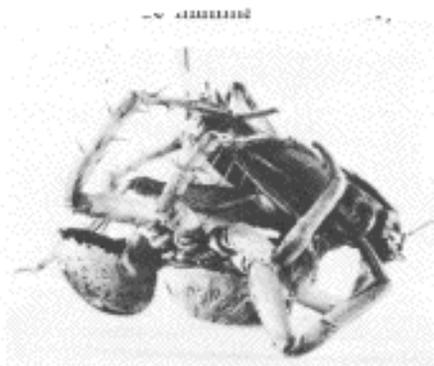
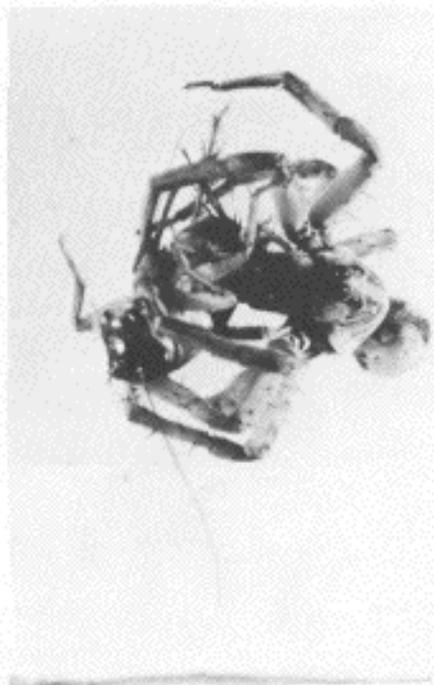


Fig. 7.—Female *Lycosa timuqua* lying inverted on the substratum after capturing a cricket.

Fig. 8.—Female *Lycosa timuqua* wrestling with a cricket as both travel in a trajectory. The pair were catapulted upward by the cricket's metathoracic legs thrusting against the substratum. (Exposure=1/2000 sec).



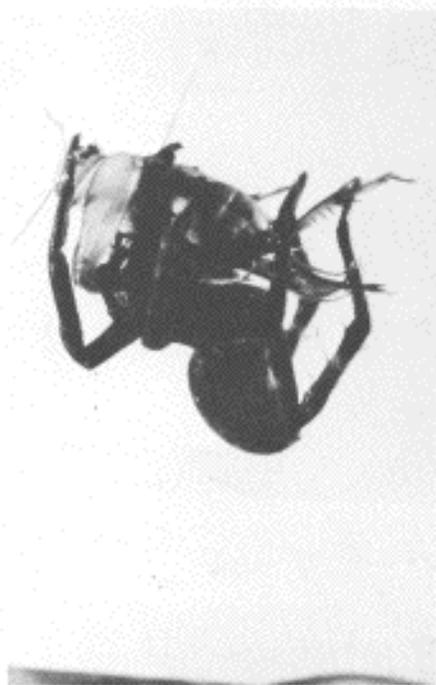


Fig. 9.—Female *Lycosa aspersa* using its distal leg segments to hang onto a cricket as both travel in a trajectory initiated by the cricket. (Exposure=1/2000 sec).

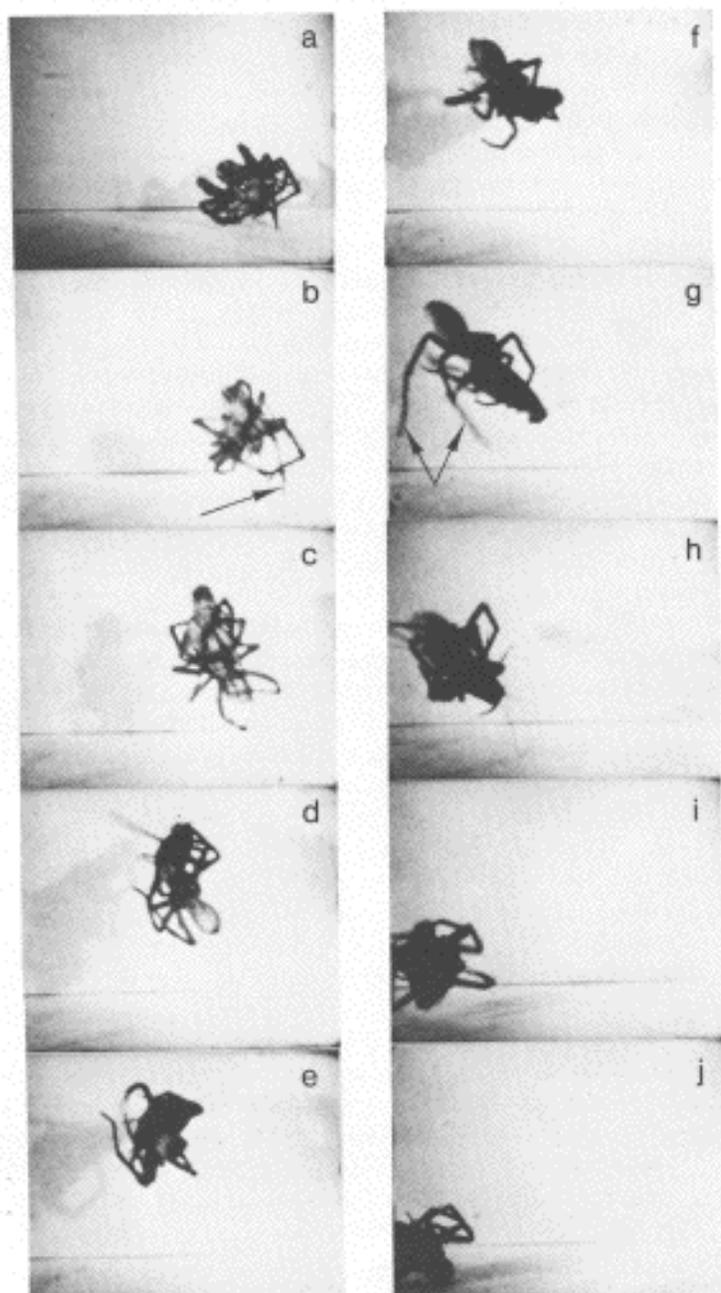


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