Observations on the Courtship Behaviour of *Lycosa carolinensis*

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Lycosa carolinensis Walckenaer (Lycosidae) is distributed throughout the eastern part of the United States. Commonly known as the Carolina Wolf Spider, it is one of the largest members of the genus *Lycosa*, the female attaining a length of 22 to 35 mm and the male 18 to 20 mm. One of the most striking physical characteristics of this species and one of the most useful in its identification is its velvety black underside, often margined in the males by a band of striking orange hairs on the sides of the abdomen. *Lycosa carolinensis* is a nocturnal hunter, but may be seen occasionally during the day roaming about grassy fields, hiding beneath stones, or in shallow burrows (to 12 cm deep), topped with turrets of silk and grass leaves. Mating occurs in the fall, with the adult males dying before winter. The females live till the next year, and possibly even a third year (Kaston, 1948). Nothing has been published concerning the courtship behaviour of the males of this species.

Rovner (1968) described the displays of males of *Lycosa rabida* Walckenaer. In his account he mentioned flexing of the forelegs and lowering of the spider's body as the most obvious characteristics of the courtship posture. As courtship proceeded, there was an alternate lifting and rotation of the palps which quivered between these rotations. Next there was an extension of one or the other foreleg (never both simultaneously) while the palpal movements continued. During foreleg extension, the palpal rotations ceased, and the palps were used to drum the substrate, producing an audible sound. Throughout this sequence, the abdomen vibrated in a vertical plane without touching the ground. Each sequence was followed by inactivity, exploration, or a slight approach towards the female. Rovner (1968) found that courtship would occur between males, but those of each pair were never observed to court simultaneously. He also observed what he called a "threat display", in which a male would raise its body high above the substrate, in contrast to the lowered position usually assumed during courtship. The possible presence of a sex pheromone was also explored, and Rovner compiled evidence to support its existence in *L. rabida.*

Kaston (1936) investigated the courtship behaviour of *L. rabida, L. helluo* Walckenaer, and *L. gulosa* Walckenaer. His account of *L. rabida* follows the same basic form as that given by Rovner (1968). For all three of the species he studied, Kaston described three basic aspects of courtship behaviour. In each case there occurred a movement or positioning of the forelegs, drumming of the palps, and vibration of the abdomen. Hegdekar and Dondale (1969) found evidence supporting the presence of sex pheromones in lycosid courtship. Their experiments with various species led them to the conclusion that the pheromone released by the female spiders was, in each case, species specific. They postulated that pheromones release sexual behaviour but do not induce copulation. In order for copulation to occur, visual and tactile stimuli or a behavioural response from the female appear to be necessary.

Vogel (1970) described the courtship displays of some species of the related lycosid genus *Pardosa.* The major elements involved in the displays described were palpal movements, abdominal vibrations and foreleg extensions. The palps were used in drumming and waving, and the front legs were elevated above the body in a typical courtship posture.

The spiders used in our experiments were collected during September and October of 1971 in Mercer County, West Virginia. They were found to be abundant in grassy fields and pastures which maintain high populations of insects, primarily field crickets. The spiders were collected at night by using a headlamp to locate the reflection from the eyes. After capture, the specimens were numbered and were housed in pint canning jars. The metal lids were replaced with screening and the jars were placed in racks on their sides. The floors of these cages were covered with 1 cm layer of plaster-of-paris containing a small amount of activated charcoal. This covering served to absorb and partially neutralize wastes produced by the spiders, and provided a suitable substrate on which the animals could rest. A small cup of aluminium foil embedded in the plaster served as a watering-dish. The spiders were watered daily and fed weekly. At first the food consisted of crickets,

but as cold weather approached and crickets became scarce, mealworm larvae from a laboratory culture were used.

Clear, rectangular plastic boxes about 12 x 25 cm were used as arenas. The bottoms of the boxes were covered with paper towelling, which was fixed in place to prevent the spiders from crawling under it. The first step in arranging a male-female encounter was to place the female in the arena. After a one or two minute calming period, the male was introduced at the farthest possible point from the female. Observations were then recorded. Male-male encounters were carried out in about the same way. Several types of pheromone experiments were used: filter paper was placed in the cage of a female overnight, then placed in an arena with a male; males were introduced into recently-vacated cages of females; and some males were placed in arenas where courtship between a female and another male had just occurred. Males used in pheromone experiments were isolated from any visual or tactile contact with other spiders for 24 hours prior to their use.

An account of a typical courtship sequence

The following account is based on average times and events drawn from 28 separate male-female encounters.

At the beginning of an encounter the female generally assumed a certain position in the arena before the male was introduced, and remained there motionless. Upon the introduction of the male into the arena, she would usually maintain this position while the male moved about.

A major movement of the female when the male was within a few centimeters, or an actual contact between the two spiders, initiated immediate reactions from the male. In cases in which the female remained motionless after the male was introduced, the males began courtship without any perceptible movement on the part of, or contact with, the female in a mean time of 3.1 minutes (range: 1-15 min.). The display of the male began when he assumed a characteristic courtship posture (Fig. 1). This position is held throughout courtship. The most obvious feature of the courtship posture is the anterior vertical extension of the first legs, which may also be observed to be flexed in a very specific way. Both legs are held above the body and are nearly parallel to each other. The tarsi point upward at an angle of about 75 degrees to the substrate. The tibiae, metatarsi and patellae are held along a straight line and at an angle of about 45 degrees to the substrate. The femorae are positioned also at 75 degrees, as the tarsi, but are not held as rigidly at this angle throughout courtship as are the other segments. The legs are relatively fixed in their vertical position, but there is a horizontal, simultaneous waving of them in opposite directions outward and back to the parallel position. From the time that the legs are positioned as described above to the end of courtship, the body is held above the substrate on the three posterior pairs of legs.

After assuming the courtship posture, the male begins other movements. Almost immediately, there is a forward movement of the palps away from the body. They are not much raised at this time, and may even touch the substrate. The palps move simultaneously from a position tucked near the body, to the position where they are normally held in non-courting males, to a final position fully extended in front of the spider (Fig. 1). No audible sounds were produced by this movement; the full extension takes less than one second. As soon as the palps reach their most extended position, there is a vibration of the abdomen and the palps return to the tucked position. The abdominal vibration consists of two distinct movements. First there is a downward twitch; the tip of the abdomen is quickly lowered, but does not appear to touch the substrate. The second movement is a vibrating return of the abdomen to its original position. The entire abdominal movement takes less than one second, and each extension of the palps throughout courtship is accompanied by an abdominal vibration.

The sequence described above is repeated two or three times while the male remains otherwise motionless. Each series is followed by a short approach toward the female, a movement orienting the head region in a different direction, or frequently nothing at all other than a pause of 8 to 10 seconds. Following this, another series of courtship sequences is begun; a single series is diagrammed in Fig. 2.

The characteristics of the male's approach depend to a great extent on the actions of the female. If the female remains motionless, the approach of the male is steady and deliberate; if the female moves suddenly

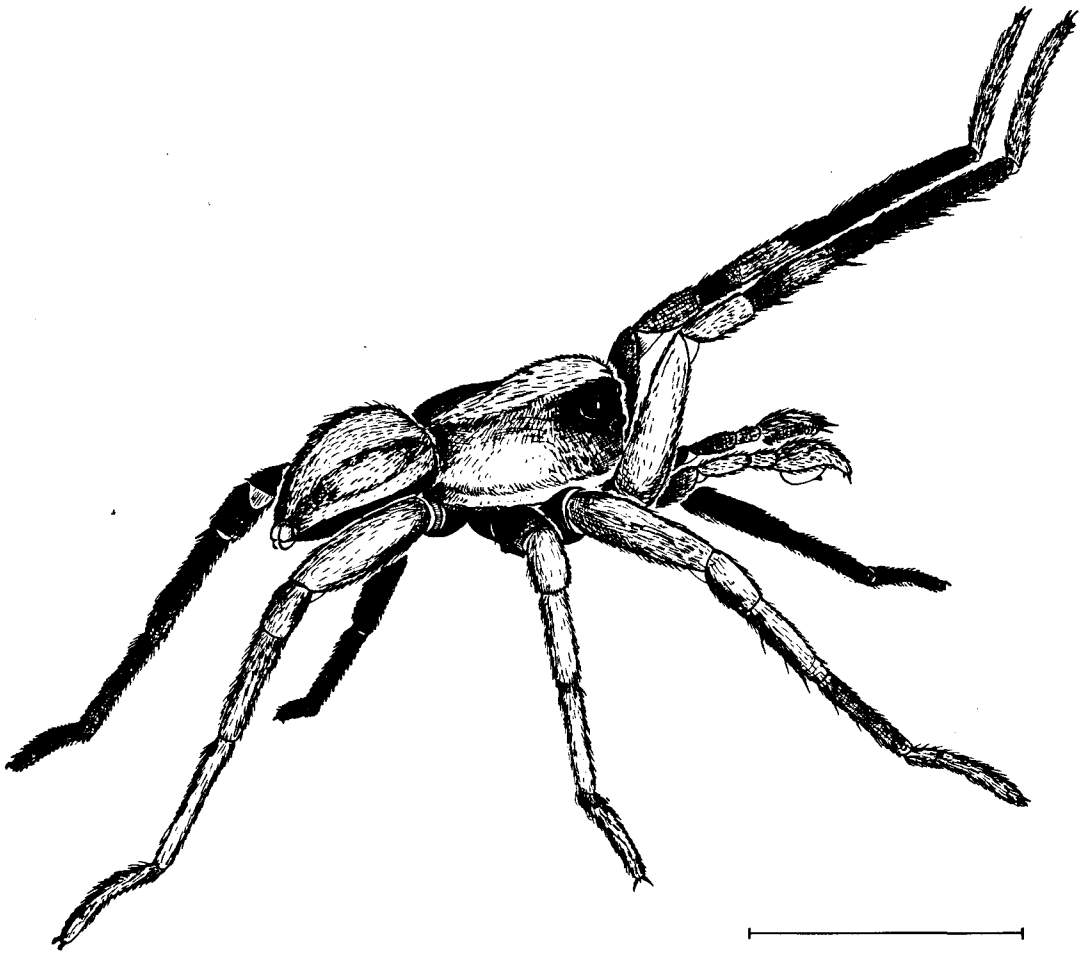

Fig. 1: The courtship posture of males of *Lycosa carolinensis*, palps in the extended position (see text), sketch by junior author. Scale line = 10 mm.

away from the male, he moves towards her quickly. If the female approaches the male, he moves slowly and cautiously. When the male is within about 30 mm of the female, he may proceed to make contact. The female is probed with either one or both of the raised first legs, which are extended and withdrawn quickly. Only the tip of the tarsus touches the female. The females we studied responded in one of two ways to the male's touch. Frequently, fighting ensued; one male was killed by a female, but usually both spiders emerged from a leg-wrestling fight unharmed. After a fight, the female usually flees, and the male follows, continuing his courtship. But if the male is pursued by the female after a fight, courtship ceases and he attempts to escape. In a second group of encounters, females fled from courting males without attacking them; the males followed and continued to court. Copulation did not occur in any of the encounters and seemed to be due to a lack of receptiveness on the part of the female. As all the females used in the study were collected as adults and later produced egg sacs, they had probably already mated in the field before being captured.

Other events of possible importance were seen in only a few courtships. The courtship movements of the males seemed to increase in intensity as the

encounter proceeds. Palpal movements and abdominal vibrations occurred every 6-10 seconds at the onset; as they continued, they became more rapid and eventually occurred as frequently as every 2-3 seconds. Contact between male and female seemed to speed up the sequences in a similar manner, no matter at what point in the encounter contact occurs. Touching the legs of the males with a wooden probe during courtship also caused a speeding up of the sequences, possibly indicating that this is a response to touch alone. During periods of re-orientation after losing contact with the female, male courtship movements ceased.

Ten male-male encounters were tried and courtship ensued in nine of them. Males began courting upon either seeing or touching another male. Simultaneous courtship was observed twice, in two separate encounters between different pairs of males.

Analysis of the courtship

The courtship behaviour of *Lycosa carolinensis* described above appears to incorporate three, and possibly four, major behavioural aspects. The use of the extended first legs seems to be a common action in all lycosid courtships thus far observed, strengthening the contention of Platnick (1971; following Bristowe) that at least some parts of spider courtship are derived from the normal search behaviour. Rovner (1968) described an extension of one or the other of the first legs of male *L. rabida* during courtship, but never a simultaneous extension, as in *L. carolinensis.* The early extension of the first legs in *L. carolinensis* seems to be triggered by the sight of the female, or the perception of a sex pheromone. Near the end of courtship, the male uses the first legs to make contact with the female; here they play a definite chemotactic role.

A second characteristic of the courtship is the vibration of the abdomen. Rovner (1968) described a similar movement in *L. rabida* males, and Kaston (1936) described abdominal vibrations in *L. gulosa* and *L. helluo*. At this time, the significance of the abdominal vibrations of *L. carolinensis* is unclear. In *L. gulosa*, the tip of the abdomen strikes the substrate during the vibration (Kaston, 1936; Harrison, 1969) producing either an audible sound or a vibration in the substrate detectable by the female. We did not observe the abdomen of *L. carolinensis* to strike the substrate, and we perceived no sounds. In fact, the body was held above the substrate in such a way during courtship (Fig. 1) as to make striking the substrate with the abdomen difficult, if not

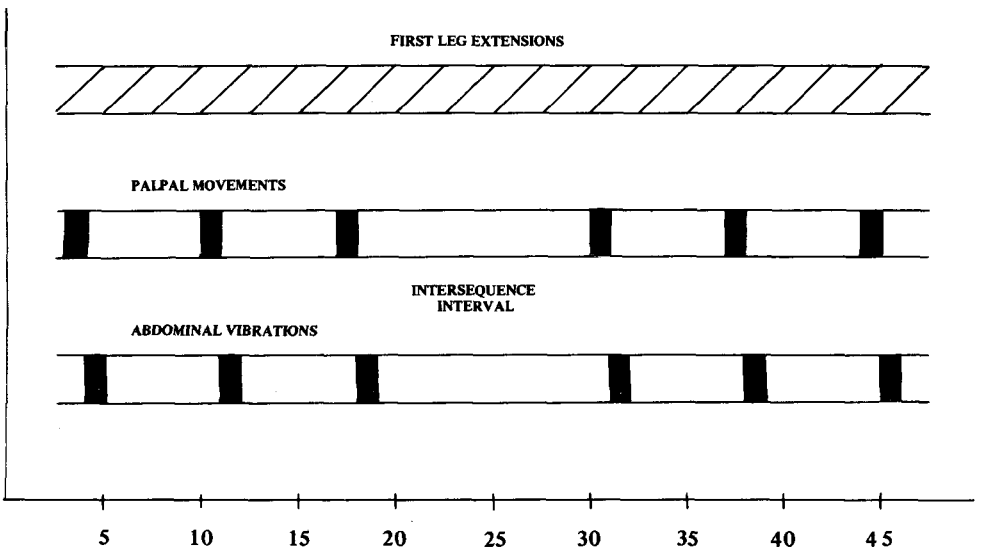

Fig. 2: A time-sequence diagram of the courtship of males of *L. carolinensis*. Scale in seconds.

impossible. A possible explanation for this difference may be found in the habitats of the two species. *Lycosa gulosa* is found on leaf-covered forest floors; the leaves provide a "sounding-board" on which the abdominal vibrations of the male produce sounds audible to the human ear at distances up to 3 m (Harrison, 1969). *Lycosa carolinensis*, on the other hand, frequents fields and pastures where the substrate is composed mostly of grasses and loose soil. Here, sound production may be difficult. The manner in which *L. carolinensis* males raise their bodies during courtship raises the line of sight. Kaston (1936) has contended that sight of the female is an important releaser in lycosid courtship. Abdominal vibration, however, may be a primitive and common feature in the courtship of spiders in general; it has been observed in almost all species that have been thoroughly studied.

The third aspect of the courtship is the palpal sequence. Rovner (1968) has shown that the drumming of the palps of *L. rabida* males produces an audible sound. Palpal drumming has also been described for *L. gulosa* and for *L. helluo* (Kaston, 1936). According to Harrison (1969), palpal drumming by *L. gulosa* is audible at distances up to 6 m. The palpal movements of *L. carolinensis* occur at the same time as the abdominal vibrations; no sounds were produced in our experiements that were audible to the human ear.[1]

The palpal movements of species of *Pardosa* are obviously visual signals (Vogel, 1970). Members of the genus *Lycosa* have poor form vision (Rovner, 1968), so precise palpal signals would probably have little importance in the courtship of these species, even though the sight of another spider might be an important stimulus in initiating the display of the male. Males of *L. carolinensis* will court other males, though they differ in colour and form from the females.

A possible fourth factor in the courtship of *L. carolinensis* is the presence of a sex pheromone produced by the female. Rovner (1968) exposed males of *L. rabida* to recently vacated cages of females, and found evidence for the production of a sex pheromone in that species. The sex pheromones so far discovered in wolf spiders all seem to be contact, rather than diffusable, pheromones.

In five out of ten cases in which males of *L. carolinensis* were placed in recently vacated cages of females, courtship behaviour similar to that described in the male-female encounters took place. This evidence, while not extremely conclusive, suggests the presence of a contact sex pheromone in *L. carolinensis*. We did not observe any cases of spontaneous courtship behaviour on the part of deprived males, but Rovner (pers. comm.) has in a few instances.

The male-male encounters seem to indicate that sight plays a role in initiating the courtship display of the male. However, the fact that males courted other males, which differ from females in size, colour and shape, demonstrates that the specific sight of the *female* is not necessary. Rovner (1968) observed a "threat display" in *L. rabida* male-male encounters; males being courted by other males responded by raising the body high off the substrate. No similar display has been seen in *L. carolinensis*, but males did appear to court one another simultaneously, and if the "threat display" is similar to courtship (see Platnick, 1971) we may not have been able to detect the differences. When courting males made contact with one another, leg-wrestling fights ensued which did not result in injury to either combatant. Separating after such a fight, males often resumed courting one another, suggesting that, not only are males unable to distinguish between males and females by sight, they cannot do so by touch either. This inference makes the role of the sex pheromone ambiguous, but perhaps it only serves to allow the males to follow females and prepares for the release of sexual behaviour on the sight of the female. Tests should be performed to determine if male wolf spiders also produce pheromones.

Acknowledgements

We wish to thank the Faculty of the Department of Biology of Concord College for their interest and help, and we particularly thank Dr Jerome Rovner,

[1] Rovner (pers. comm.) has recorded on tape a single instance of sound production by *L. carolinensis*, and has detected sound production in all *Lycosa* species he has examined. We were unable to perform additional experiments to confirm this because of a lack of specimens in the unusually wet summer and fall of 1972.

Ohio University, Athens, Ohio, USA, for his helpful suggestions and for access to unpublished observations.

Summary

Seventy-one encounters between individuals of *Lycosa carolinensis* Walckenaer were observed. Male-female encounters, male-male encounters, and sex pheromone experiments were performed using adult spiders captured in the field. The courtship behaviour of the males involved extension and simultaneous horizontal waving of the first legs, typical palpal movements and abdominal vibrations. No sound production was detected, but remains a possibility because of the limitations of the experiments. Copulation was not observed. Males were seen to court each other simultaneously, as well as alternately. Some evidence was gathered which supports the presence of a sex pheromone produced by the females.

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Two spiders of the genus *Erigone* Audouin from New Zealand

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The following is an account of eleven specimens found in New Zealand of the genus *Erigone* given to me by Mr C. L. Wilton under the label "18.VI.70. Parkes - Valley Nelson. 369064. N. A. Martin." Five are males (here labelled 1 to 5) and six are females (6 to 11). In view of their having been introduced into the country their occurrence and possible origin is of interest. Two species are present: *Erigone prominens* Bösenberg and Strand, and a new species, here named *Erigone wiltoni* sp.n.

Erigone prominens Bösenberg and Strand

Two males (2 and 3) have been compared with specimens from Japan in the Senckenberg collection (Frankfurt). The species is described by Oi (1960, p.180) the leg measurements he gives are somewhat shorter than those of the Senckenberg specimens of the same carapace length. While his Fig. 175 does not show the teeth present on the dens medius of the embolic division of the palpal organs, it otherwise agrees with the Senckenberg specimens; these are bleached white and are difficult to examine, but this outline is clear enough and it agrees closely with the corresponding outline in the New Zealand specimens 2 and 3. (It seems clear that the inside of the tibia viewed from exactly the same position appears very much the same in all these species and is not likely to be very useful in separating them). The figure of the palp given by Bösenberg and Strand in 1906 is small, but that by Strand (1918, Tab.II Fig. 21) is good and shows clearly the teeth on the dens medius, as well as the patella length and form of the carapace. Another species described by Oi (ibid. p.181) is *E. koshiensis* Oi, which is close to *E. prominens*, but differs in the position of the metatarsal trichobothrium (Tm. 1 = 0.53).