1-1-1996

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1996. The Journal of Arachnology 24:141–147

HABITAT AND COURTSHIP BEHAVIOR OF THE WOLF SPIDER *SCHIZOCOSA RETRORSA* (BANKS) (ARANEAE, LYCOSIDAE)

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ABSTRACT. The habitat and courtship behavior of the wolf spider *Schizocosa retrorsa* (Banks 1911) were studied and are described here for the first time. The range of *S. retrorsa* was extended to include the lower peninsula of Michigan. This species is locally abundant in highly exposed habitats of sand or pine litter. Male courtship consists of chemoexploration, palpal drumming, an extended leg tap, and a "push-up" display. Female displays include a double leg arch, approaches, and orientations toward the male.

Courtship behavior in spiders has been of interest to arachnologists for some time and continues to be a common area of study (Peckham & Peckham 1889; Kaston 1936; Rovner 1968; Stratton 1985). The visual signals of the brightly colored Salticidae and the large Lycosidae have probably made them particularly conspicuous to human researchers. Along with the rather conspicuous visual signals, lycosids have also been shown to use acoustical or vibrational communication through the use of a palpal stridulatory organ (Rovner 1975). The importance of chemical communication has also been investigated (Tietjen 1977, 1979). However, the relative importance of visual, chemical, tactile, and acoustical or vibrational communication in any one species or habitat has only recently been addressed (Scheffer et al. in press).

Some of the most comprehensive studies of spider courtship have been conducted with species within the wolf spider genus *Schizocosa* (Kaston 1936; Montgomery 1903; Hegdekar & Dondale 1969; Uetz & Denterlein 1979; Stratton & Uetz 1981, 1983; Rovner 1973; Stratton 1982; and Stratton & Lowrie 1984). Courtship behavior has been described for a handful of *Schizocosa* species, primarily in the *S. ocreata* species group. The role of male courtship behavior as a reproductive isolating mechanism has proven to be very important in at least two species. *Schizocosa ocreata* (Hentz 1844) and *S. rovneri* Uetz & Dondale 1979 are reproductively isolated due to their courtship behavior (Stratton & Uetz 1981, 1983, 1986; Uetz & Denterlein 1979; Stratton, Miller, & Hebets unpubl. data). When forcibly mated, interspecies hybrid offspring are also reproductively isolated by behavior (Stratton & Uetz 1986). *Schizocosa ocreata* and *S. rovneri* are thus termed "ethospecies", i.e., species reproductively isolated by behavioral mechanisms of courtship (Hollander & Dijkstra 1974). The acoustical components of *Schizocosa* courtship are crucial to the reproductive isolation of these ethospecies. It has been suggested that this acoustical variation may, in part, be due to habitat differentiation (Stratton & Uetz 1986).

Schizocosa retrorsa (Banks 1911) is widespread and is known from 38 collections from the midwestern and eastern United States (Dondale & Redner 1978). Although Dondale & Redner (1978) offer a description of this species, little is known of its ecology and behavior.

Here we provide an analysis of the male and female courtship behaviors of *Schizocosa retrorsa* and discuss the possible impact of the habitat of this species. The behavior of *S. retrorsa* is of interest because it is not a member of the *S. ocreata* species group. *Schizocosa*

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retrorsa occurs in a different habitat from the *S. ocreata* group, and the male secondary sexual characteristics (seen as black brushes of hair on the male forelegs, pigmentation on male forelegs, etc.) are different from those species previously studied.

METHODS

Specimens.—Penultimate and mature males and females were collected at night from five sites in Lafayette, Marshall, and Panola Counties, Mississippi and one site in Berry County, Michigan between 15 June–29 June 1993. Collection sites were **MISSISSIPPI**: *Lafayette County* --University of Mississippi campus, Old Taylor Road near baseball stadium T8S R3W Sect. 29, 34°21′N 89°32′30″W; and 8 mi. SE Oxford T10S R3W Sect. 35, 34°36′N 82″29′W. *Marshall County* --3.8 mi. N of N end of Tallahatchie Bridge on Old Highway 7. T6S R3W Sect. 2, 34°36′N 89°29′W; and 1 mi. N of Wall Doxey St. Park on pipeline E of Hwy 7. T5S R3W Sect. 1, 34°40′N 89°28′W. *Panola County* --near Sardis Dam. T8S R6W Sect. 13, 34°23′N 89°47′30″W. **MICHIGAN**: *Berry County* --Deep Lake Campground, Yankee Springs Recreation Area. Specimens from this study are housed at the University of Mississippi. Voucher specimens are deposited in the Mississippi Entomological Museum at Mississippi State University.

The spiders were transported to the laboratory and held individually in 8 cm × 4 cm plastic cages in a controlled environment (21 °C and 12L:12D cycle). Water was provided via a cotton wick dipped into a reservoir below the cage. Spiders were fed several small crickets approximately twice each week.

Behavioral observations.—Between 23 June–15 July 1993, we videotaped interactions of 23 pairs of mature males and females (all of which were between 8–23 days post maturation molt). Females were removed from their cages approximately 12 hours before a pairing and were placed on filter paper in culture dishes. Prior to recording, the female and filter paper were transferred to a 9.5 cm transparent cylindrical observation arena. The filter paper was positioned in such a way that approximately 0.5 cm of it extended beyond the wall through a slit at the bottom of the cylindrical arena. A sound transducer (stereo needle) was placed on the protruding edge of the paper. The female was constrained within a 4 cm transparent barrier inside the observation arena that could be removed when appropriate. The male was gently introduced into the arena through a 20 cm long 1.5 cm diameter glass tube.

Video recordings were made with a Panasonic HD-5000 video camera with either a 105 mm macro (1:1, f/2.8) lens for close-up recording of the male or a 10.5–125 mm zoom (1:16, 12×) for sequences involving both the male and female. Stridulatory sounds were recorded from the substratum with a stereo needle transducer attached to an EG & G PARC, Model 113, preamp (Gain set at 5K, low roll off set at 0.3Hz, high roll off at 10kHz) and overlaid onto the videotape.

Video and acoustic recording began when the male was introduced and continued for approximately 10 min. If no courtship was seen, the male was scored as "negative" and was replaced. If a male showed courtship display, the females were watched closely for signs of receptivity (e.g., jerky walk, pivots, orientation toward the male). If a female seemed to be receptive, the barrier was lifted and the male and female were allowed to interact.

Seven copulations were observed. When copulation occurred, it was videotaped for 10–45 min. Total times of copulation were recorded for two of the pairings. Most of the copulations were recorded on videotape for only a short period of time, after which the pair was removed from the camera's field of view (these spiders were allowed to continue copulating). After each pairing, the observation arena was swabbed with alcohol.

Analysis of behavior.—Of 23 male-female pairings, 20 were scored (three tapes could not be scored due to camera angles). The pairings were first separated into four categories: pairings that ended in copulation (n = 7), pairs with males that courted but did not copulate (n = 5), pairs that neither courted nor copulated (n = 5), and pairings in which the female was aggressive towards the male (n= 3).

A one minute video sequence for each pairing was scored for sequences of actions, repetition of behaviors, intervals between behaviors, duration of behaviors and, when feasible, positions of both males and females. For the pairs that copulated, the scored minute was that minute directly preceding the mount by the male. Males will begin their courtship

when simply introduced to a female pheromone and do not necessarily immediately orient to a female when one is present; thus courtship or orientation cues did not provide good starting points for analysis of behavior. For the pairs that did not copulate, the scored minute was a segment of tape which included a courting male and a female after removal of the barrier. No criteria were used for choosing the scored minutes of non-courting pairs. The scored minute for the pairings with the aggressive females directly preceded a "lunge" towards the male by the female.

The six behaviors that we examined closely in comparing these courtship displays were: male "push-ups", male extended leg taps, female double leg arches, female approaches, female orientations, and male orientations. Instances in which the males displayed a "defensive stance" when confronted with an unreceptive female were also noted.

Statistical analysis.—Two tailed *t*-tests were done on the frequencies of male extended leg taps, male "push-up" displays, and female double leg arches to compare the frequencies between pairs that copulated and pairs that only courted.

RESULTS

Habitat.—The first Lafayette County, Mississippi site was a mowed sandy hillside adjacent to a major road; a second site was in an open pine woods (Lafayette County); third and fourth sites were exposed "borrow pits" which were sandy with lichens (Marshall County & Panola County); and a fifth site was a sandy grassy pipeline along the highway (Lafayette County). The Berry County, Michigan site was an open sandy field.

Description of courtship.—The male courtship consists of four basic displays: (1) chemoexploration, (2) palpal drumming, (3) extended leg tap, and (4) "push-up".

In the pre-courtship display (the "searching phase"), males walk around the arena until they come into contact with female silk, after which the male exhibits chemoexploration (Stratton & Uetz 1983). In chemoexploration, males move the palps by rubbing the dorsum of the palp against the substratum in a circular motion as described by Tietjen (1979). The display typically lasts only a few seconds. The behavior is used presumably for detecting pheromones that may have been left by a female and takes place almost immediately when a male is introduced to female silk.

Chemoexploration was typically followed by palpal drumming (1–3 drums/sec). In this behavior, the male quickly lifts and lowers his palps as if they were beating on a drum. There is sound produced during this display, but we cannot state whether the sound is made strictly from the drumming or from stridulatory organs located in the palps. The male stands motionless during palpal drumming with the long axis of the body parallel with the substratum. Bouts of palpal drumming are interspersed with rest periods. Palpal drumming takes place even when a female is not physically present.

As palpal drumming continues, the male displays an extended leg tap. In this display, the right or left leg I is lifted, extended, lowered, and then tapped on the substratum at a rate of several taps per second. Each tap brings the leg nearly perpendicular with the substratum. It is not clear if the leg comes in contact with the substratum or not. There is sound accompanying the extended leg tap, but the sound has not been verified as to be coming from the palps (tapping or stridulation) or from contact of leg I on the substratum. The extended leg tap gives a strobe effect due to the contrast between the black femur of the foreleg and the white of the tibia.

The fourth display in the male's courtship is the "push-up" behavior. This behavior is given when the male turns to orient towards a female or when he is resuming his palpal drumming after a pause. During the push-up display, the male begins with his body lowered to the substratum and displays palpal drumming. He lifts his entire body up onto the tips of his legs. During the lifting of the male's body, a loud stridulation, almost a click, is audible. It is not obvious how the clicking noise is made.

We identified two distinct female behaviors: (1) double leg arch, and (2) approach. In the double leg arch, the female lifts legs I and II on either her right or left side. As the legs are lifted into the air, the femurs are nearly perpendicular to the long axis of the body carapace and the bending ("arching") occurs at the femur-patella joint and the tibia-metatarsus joint; the femur, tibia, and tarsus form three sides of a square.

Females of *S. retrorsa* also display an ap-

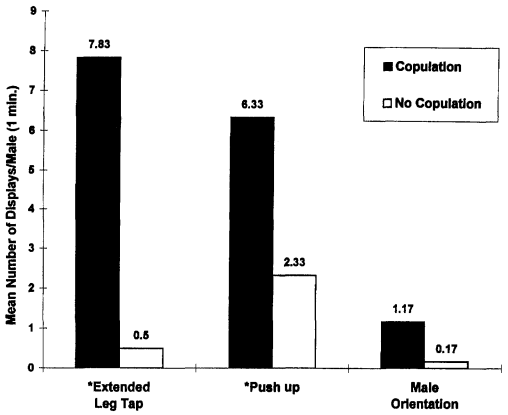

Figure 1.—Comparison of the frequency of three male courtship displays between pairings that ended in copulation and pairs in which the male courted but no copulation occurred. (★) indicates that there is a significant difference between pairings that copulated and those that did not.

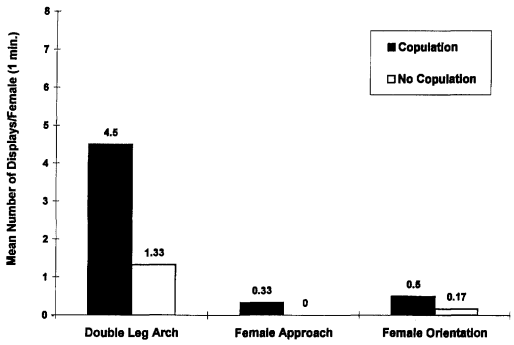

Figure 2.—Comparison of the frequency of three female courtship displays between pairings that ended in copulation and pairs in which the male courted but no copulation occurred.

proach behavior. A receptive female will approach a stationary, courting male either from the side or from the back. The approach is very slow and seemingly deliberate, often with double leg lifts intermittently displayed. On a few occasions, the female turns and orients herself directly in front of a courting male, placing herself in what is apparently a pre-mounting position.

The mount of the male onto the female is very rapid; there is no grappling. During copulation, the male inserts a palp several times on each side (seen in all seven pairs that copulated) with disengagement of the palp after each hematodochal expansion. This is followed by a switching to the opposite side, where there are once again multiple insertions. The female rotates her abdomen laterally so that the male genital bulb can come into contact with her epigynum.

Analysis of behavior.—The spider pairings that ended in copulation showed a significantly higher number of extended leg taps ($t = 3.62$, $df = 9$, $P < 0.05$) by the male than pairs that courted but did not copulate (Fig. 1). The number of push-up displays by the male between these two pairings was also calculated to be significantly different ($t = 2.29$, $df = 9$, $P < 0.05$).

The mean number of double leg arches by the female appears much larger in pairs that copulated (Fig. 2) but there was no statistical difference ($t = 1.02$, $df = 9$, $P < 0.05$). The double leg arch was also observed in aggressive females.

Neither push-up displays, leg taps, nor orientations by either sex were seen in the non-courting pairs nor when the females were aggressive. Both male and female orientations toward the opposite sex were seen most frequently in pairings that ended in copulation (Figs. 1, 2). The latency to copulation of the pairs mated in the laboratory ranged from 5 min, 13 sec (00:05:13 min) to 1 h, 18 min, 1 sec (01:18:01 min). A flow chart showing the frequency of different sequences of male and female displays gives a visual image of the patterns of behavior that occur in both sexes throughout the courtship display (Fig. 3).

Copulations and egg sacs.—In 17 of 23 pairings, males showed courtship displays (74%). Seven of these courtship displays ended in copulation and three of the mated females produced egg sacs. In three pairings, the female was aggressive; and in two of these cases, the males were killed by the female.

Copulations were observed in the laboratory during the period of 23 June–8 July, covering a two-week time span. Two copulations, excluding any courtship, were timed with the first lasting 2 h, 30 min (02:30:00 min) and the second lasting 2 h, 40 min (02:40:00 min). The three females mated in the laboratory produced their egg sacs 25, 28, and 40 days, respectively, after copulation ($\bar{X} = 31$ days, SD = 7.9).

Seventeen of the females that were mature upon collection, but not used in any laboratory trials, produced egg sacs. For these females, the time from their collection to egg

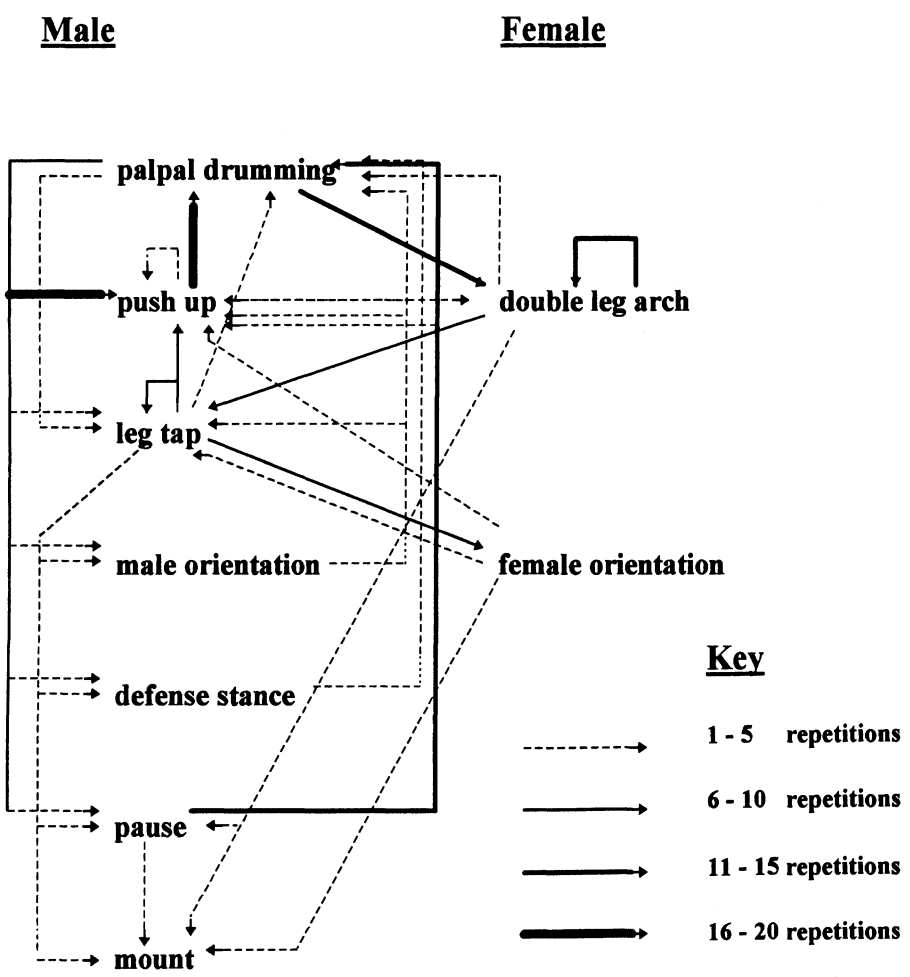

Figure 3.—Flow chart of male and female *Schizocosa retrorsa* courtship displays.

sac production ranged from 21–63 days ($\bar{X}$ = 33 days, SD = 10.4).

Four of the 17 females produced a second egg sac after having lost their first. The second egg sacs were produced between 24–30 days after the first sac was dropped ($\bar{X}$ = 25.5 days, SD = 3.5). Most of the egg sacs were abandoned by the females during shipment from Mississippi to Michigan in the middle of August 1993. Two females successfully hatched young 42–45 days respectively after egg sac production.

DISCUSSION

Habitat.—Species of *Schizocosa retrorsa* tend to be found in highly exposed areas in the presence of sand or pine needles. It is possible that sand and pine needles play some role in camouflaging the spider, thus aiding in their protection. The light sandy color of the legs would seem to blend in quite well with sandy ground or dead pine needles. The broken bands along the carapace, seen as dots, could also aid in this blending. Although the entire body of the female is a light sandy color, the male possesses very distinct black pigmentation on his femur of legs I. This femur not only greatly contrasts with the sandy color of the ground, but it also contrasts with the light color of the male's tibia. This distinct contrast on the forelegs of the male, we believe, aids in his attempt to attract the attention of a female. As male spiders spend most of their lives as immatures with the same camouflaged coloration as females, this pigmentation may be linked to courtship as it is only

upon reaching sexual maturity that they no longer blend in with the environment.

It is apparent that sound as well as vision constitutes a large portion of courtship for this particular species. Many members of the genus *Schizocosa* stridulate, yet few show palpal drumming (*S. mccooki* (Montgomery 1904) shows "bursts" of percussion; Stratton & Lowrie 1984). It is possible that the substratum upon which these species are found is the best conductor for their particular courtship sounds. Sand or pine needles may transmit the acoustical signals most effectively for *S. retrorsa*. Further work is needed to test this hypothesis.

Courtship.—Much of what is known of the courtship rituals of different species within the genus *Schizocosa* suggests that courtship tends to deal a significant amount with the foreleg patterns of the male spider. Since the mature males of *S. retrorsa* have black pigmentation on the femur of their forelegs, it is not surprising that this generalization holds true for this species also.

The extended foreleg tap of the male is apparently a key display in the success of his courtship. In two instances (Fig. 3) the leg tap directly preceded a successful mount by the male. This extended leg tap is a striking display that is presumably very conspicuous to female spiders. The significantly larger number of extended leg taps displayed by males that eventually copulated supports the notion that this display is of great importance in the success of male *S. retrorsa* courtship. Once again, further research is needed to pinpoint exactly what it is about this behavior (vigor, intensity, frequency, etc.) that makes males more or less successful.

Although the male push-up display is apparently important in courtship, it does not seem as tightly linked to copulation as is the extended leg tap. The push-up display seems to be a starting point for males; it normally follows a long pause or a male walk or turn. Since the push-up display was seen only in males that courted and in every courting male except one, it is apparently an integral part of male courtship. There may be a certain ratio between extended leg taps and push-up displays that is most effective for courting males.

The female displays are a bit more difficult to interpret. The female orientation and approach seem to be clearly linked to copulation. The approach by a female was only observed in pairs that copulated and female orientations were observed only in the presence of a courting male. However, the female double leg arch is seen not only in the presence of courting males, but it was also displayed by aggressive females. Using the term "female courtship" for the female double leg arch display may not be very accurate. Perhaps unreceptive females are engaging in this "receptive" behavior in order to entice a male to approach and thus ensure a meal.

Copulation.—The relatively long duration of copulation (2–3 h) in *Schizocosa retrorsa* is similar to that in other members of the genus. These spiders may incur a higher risk of predation by engaging in copulation for several hours on the forest floor; there must be a benefit for this long copulation (e.g., fertilization, etc.), but it is yet unknown.

The pattern of palpal insertion during copulation for *S. retrorsa* is also similar to that in other members of the genus in that there are several insertions per side with palpal disengagement between hematodochal expansions (Rovner 1973).

ACKNOWLEDGMENTS

This work would not have been possible without the help of Patricia R. Miller who found several of the localities for this species and helped with identifications. For this help we are most grateful. We also wish to thank W. Miller and K. White for their assistance collecting spiders and W. Davis for her support and helpful insights. The comments of G. Uetz were very helpful in the writing of this manuscript. Financial support was provided by a grant from the National Geographic Society #4916-92 to G. Stratton and G. Miller.

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Manuscript received 8 September 1995, revised 5 February 1996.