LIFE CYCLE AND COURTSHIP BEHAVIOR OF THE BURROWING WOLF SPIDER *GEOLYCOSA TURRICOLA* (TREAT) (ARANEAE, LYCOSIDAE)

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ABSTRACT

  The life cycle and male and female courtship behavior of the burrowing wolf spider *G. turricola* are
described. *Geolycosa turricola* is found to have a two-year life cycle rather than the one-year cycle
previously reported. Copulation occurs in late summer following a period of cohabitation of the
mature male and a penultimate female. Spiders were collected during cohabitation and the courtship
video recorded. Male *G. turricola* engage in a series of leg waves and body movements followed by a
copulatory position face down in the burrow of the female. The courtship pattern is generally similar
to that of other lycosids except for the lack of palpal waving and abdominal movements. It is thought
that cohabitation provides a pre-courtship opportunity for sexual communication thereby mitigating
the loss of some elaborate display elements.

INTRODUCTION

  Courtship behavior among wolf spiders (Lycosidae) involves patterns of leg and
palpal movements and abdominal vibrations (Bristowe and Locket 1926; Kaston
1936; Rovner 1968) and often includes the exchange of chemical cues and the
production of substrate vibrations and acoustic signals (e.g., Uetz and Stratton
1982; Tietjen and Rovner 1982). However, considerable variation in courtship
pattern exists among lycosid species (Platnick 1971), and little is known of the
specifics of the courtship of groups that have adopted unusual life strategies such
as burrowing and web building (e.g., *Geolycosa* and *Sosippus*). Here we describe
the phenology and basic courtship behavior of the obligate burrowing wolf spider
Geolycosa turricola (Treat). We compare the behavioral characteristics of this
species to those described for other wolf spiders and discuss the importance of

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variation in courtship patterns among burrowing and non-burrowing forms in relationship to the burrowing life strategy.

The genus *Geolycosa* is distributed widely throughout North America, with the greatest species diversity occurring in the southeastern United States (Wallace 1942). *Geolycosa turricola* (Treat) is one of the most widely distributed species and is found in New England, along the eastern seaboard, in Northern Florida and in the Florida panhandle (Wallace 1942). We have discovered several populations in central Mississippi.

Geolycosa generally prefer well drained or sandy habitats (Wallace 1942; McCrone 1963). The spiders construct burrows shortly after dispersing from their mother's burrow and are thought to remain in the same burrow for life, enlarging it as they grow (Wallace 1942; McQueen 1983).

MATERIALS AND METHODS

The life cycle of *Geolycosa turricola* was deduced from periodic observations of populations in Oktibbeha County, Mississippi and Santa Rosa County, Florida over a period of four years.

Courtship was observed in 10 pairs of *G. turricola* that were collected in August 1984 in Oktibbeha County, Mississippi about 12.8 km north of the Mississippi State University campus. A detailed description of the habitat and dynamics of that population is being prepared (Miller and Miller, in prep.). We have reported that *G. turricola* engage in a period of pre-courtship cohabitation in which mature males and penultimate females share the female's burrow (Miller and Miller 1986). The spiders used in this study were collected during that time, returned to the laboratory, and held until the females matured.

Penultimate females were provided with artificial burrows constructed of paper half-cylinders that were situated in sand with the open side of the cylinder against the glass of 75 L aquaria. The females adopted the burrows without hesitation and, in each case, lined the paper burrow with silk. Movements of the females inside their burrows were difficult to observe in this setup because the females deposited silk on the glass thus obstructing our view. However, females could be easily observed when they positioned themselves at the burrow entrance, the typical position during courtship (see below). Females constructed turrets at the burrow entrance with bits of grass that were provided. Males were held in wire cages adjacent to the burrow of their mate. Each of the females molted successfully to maturity.

Courtship was allowed to proceed (male was released from his cage) within 24 h after the final molt of the female. The courtship bouts were video recorded. Video tapes were analyzed with the aid of a multiple event timer computer program (DeAngelis and Miller 1985). Field observations indicated that courtship takes place in the early evening hours and, thus, most courtship bouts were recorded between 1800 and 2000 h. Recordings were made in low room lighting, and the laboratory temperature was around 22°C. No attempt was made to record sounds made during courtship. Copulation was allowed to continue until termination at which time the males were removed for further experimentation.

Twenty-four h after completion of copulation, one-half of the males were reintroduced to the female with which they had previously copulated, and one-half to a strange and previously mated female. The courtship behavior of these

pairs was observed to determine if mated females would accept a second male and if males would court females with which they had not cohabitated (second group of five). Each of the ten males was also introduced in turn to mature females without burrows, to empty burrows previously occupied by mature females, and to turret material from burrows of mature females. The difficulty in finding and collecting mature males made reuse of the males for these latter experiments a necessity.

RESULTS

Life cycle.—Emerton (1912) believed that *Geolycosa turricola* completed its life cycle in one year. Wallace (1942) concurred and reported finding mature males in spring and early summer (May to July) in Florida. These observations are not consistent with those we have made in Mississippi. We believe that *G. turricola* has a two year life cycle with copulation occurring in late summer (August and September). Females overwinter and produce young in spring (late April through June). Those young overwinter and mature in their second summer. This is consistent with the pattern of other *Geolycosa*; e.g., *G. fatifera* (Hentz), *G. missouriensis* Chamberlin, and *G. pikei* (Marx) (Wallace 1942).

Pattern of courtship behavior.—Male courtship was typically of short duration ($\bar{x}$ = 1.2 min, SD = 0.78, n = 10). Two distinct phases in male courtship are distinguishable: (1) approach, and (2) contact. Prior to their release, males engaged in a brief exploration of their cages and then oriented toward the female's burrow. Unless disturbed, males remained in that position until released.

The approach phase includes those behaviors of the male that occur at a distance beyond the reach of the female's forelegs and as part of his movement toward her. Several separate approaches may be made by the male depending on the intensity of the aggressive behavior of the female (Fig. 1).

An approach may include combinations of four distinct behaviors: (1) foreleg-waving, (2) foreleg-tapping, (3) retreat, and (4) palpal-drumming. During a foreleg-wave, the leg is drawn back, raised, stretched high above the cephalothorax (Fig. 2), and then lowered. The legs are often waved alternately in a "bicycling" motion. No palpal drumming or abdominal vibrations are observed during foreleg-waves. The male walks toward the female's burrow during leg waves.

Foreleg-tapping behavior is interspersed with foreleg-waving. Foreleg-tapping, which the male performs while in a stationary position, involves quick, jerky downward "taps" of one or both forelegs (on occasion one of the second legs will tap simultaneously with the first leg on the same side). The forelegs do not touch the ground during the taps. The legs are held high for this part of the display (Fig. 2 shows a typical starting position for a leg tap). Leg waving movements of the female (described below) that are given during male leg-waving may cause the male to stop and engage in leg-tapping.

If the female displays aggression (described below) toward the approaching male, the male quickly retreats and immediately engages in palpal-drumming movements. The male's palps were never observed to make contact with the sand substrate of the aquarium. In the retreat behavior, the male quickly steps or jumps back and lowers his body to the ground (similar to the posture shown in Fig. 2). The male remains in this position only for a short time before resuming
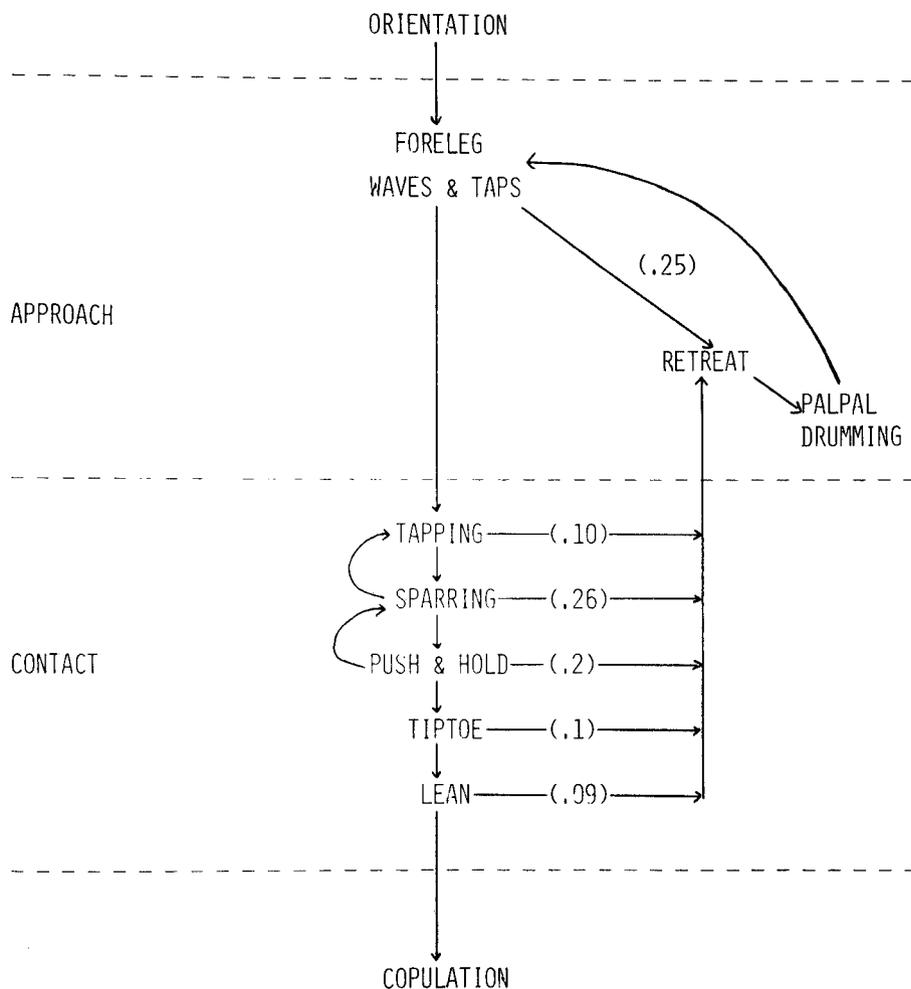
Fig. 1.—Sequence of elements of courtship behavior of male *Geolycosa turricola*. Numbers in parentheses indicate the proportion of the total number of retreat moves that were initiated at various places in the sequence. Behaviors are explained in the text.

his approach ($\bar{x}$ = 7.25 s, SD = 3.1, n = 31, n refers to the total number of retreats observed in the 10 males studied). Males may retreat at any point in the courtship sequence in response to aggression by the female. However, two-thirds of male retreats occurred during approach or early contact (tapping and sparring, Fig. 1).

The contact phase of the male courtship is that period when the male and female are close enough to each other to touch. Contact courtship may be interrupted by aggressive moves of the female that prompt the male to initiate another approach or to return to an earlier behavior in the contact courtship sequence (Fig. 1). The contact phase involves five distinct behaviors: (1) leg-tapping, (2) sparring, (3) push-and-hold, (4) tiptoe, and (5) lean.

Leg-tapping movements of the male during the contact phase are functionally similar to those described above except that individual "taps" often make contact with the female's forelegs or cephalothorax. Leg-tapping by the male stimulates
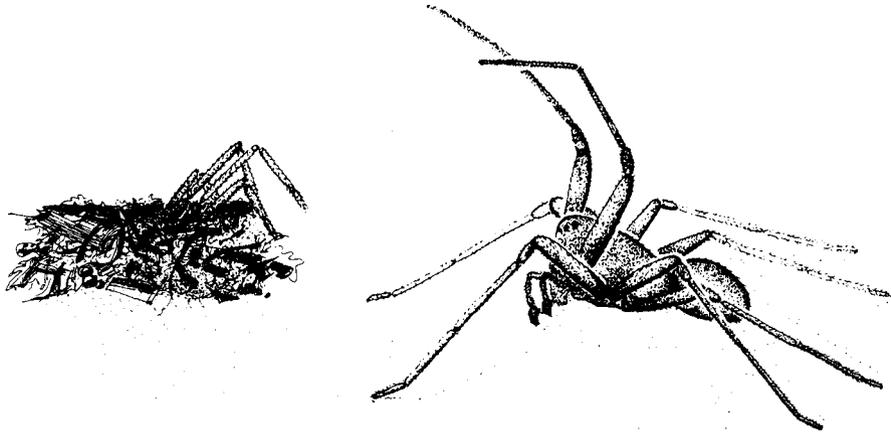
Fig. 2.—Approach of courting male *G. turricola*.

the female to engage in foreleg sparring with him. During sparring, the male attempts to push the female's forelegs down and hold them against the turret in what we term the push-and-hold behavior. If he succeeds in holding her forelegs down, he begins the tiptoe movement in which he raises his body high above hers (Fig. 3). This is the first time during courtship (with the exception of instances where female attacks take her out of her burrow; see description below) that the female would be able to see the proximal portions of the male's forelegs, his venter, and his palps (Fig. 3). The male engages in no palpal or abdominal movements during this time.

If the female shows no aggressive behavior, the male begins to lean forward into the burrow from the tiptoe position. This behavior involves "walking" his forelegs across the female's back and, thus, requires that he release his hold on her forelegs (Fig. 3). The successful male will eventually adopt a copulatory position face down in the burrow.

Behaviors during the contact phase always occur in a specific sequence (Fig. 1). The sequence may be interrupted at any step by aggressive displays of the female. If the male is interrupted during the tapping behavior (25% of total retreats were initiated during this time), he will retreat and begin a new approach. If the contact courtship sequence is interrupted during tapping, the male retreats (10% of total retreats) and begins another approach. Interruption of the male during sparring or the push-and-hold phase prompts the male to either retreat (26% and 20% of total retreats respectively) and begin another approach or to return to the previous behavior in the contact sequence (e.g., he will return to sparring if he is interrupted during the push-and-hold). Our observations indicate that the more intensive the female aggressive behavior that initiated the break in the sequence, the more likely it is that the male will retreat and begin a new approach. If the contact sequence is interrupted during the tiptoe or the lean, regardless of the intensity of the female aggressive behavior, the male retreats and begins a new approach.

In a typical courtship bout, the female adopts a position at the burrow entrance just below the rim of the turret. In this position, her forelegs, which are draped over the turret, could be visible to the approaching male, but she cannot
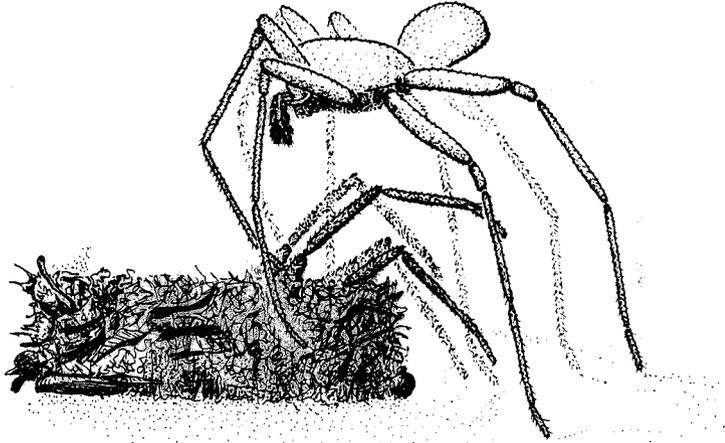
Fig. 3.—Tiptoe behavior (beginning of the lean behavior) of male *G. turricola.*

see the male (Fig. 2). As the male moves into contact range, the distal portions of his legs (which are held high) come into her field of view.

Females engage in several distinct behaviors during courtship: (1) leg-waving, (2) sparring, (3) attack, (4) quiescence. Female leg-waving is not as distinctive a behavior as that of the male. Female leg-waves consist of gentle, slow up and down movements of one or both first legs. These waves, like the male leg-waves, are given during the male's approach phase.

Female aggressive behavior may take the form of an overt attack or may consist of quick leg movements. Aggressive behavior is observed during both the approach and contact phases of courtship. During an attack, the female lunges from her position just below the turret rim to a position with her midsection over the turret, her first legs raised high and her chelicerae spread. From this position, she is able to see the male. The female is quiescent during most of the courtship. We observed no significant palpal movements by the female.

Variations in typical courtship pattern.—In two instances females remained below the burrow entrance (out of the male's visual field) during male approach. In these two cases, the male engaged in a normal approach (presenting leg-waves and leg-taps but no retreat or palpal-drumming behaviors). When the male reached the burrow entrance, he slowly probed the tunnel with his forelegs and proceeded into the tunnel until he made contact with the female. The female reacted by gently pushing the male out of the burrow. When the male had backed out of the burrow and the female had reached the entrance, she engaged in an attack. The male retreated and then began another approach.

In one of these two cases, the female dropped back below the turret rim but remained at the entrance (Fig. 2), and the male proceeded with courtship display. In the other case, the female retreated to the bottom of her burrow after the first attack, and the male was forced to coax her out a second time before courtship could proceed. Copulation occurred in both cases.

Copulation.—Except for the burrow entrance, which is somewhat flared, the diameter of *Geolycosa* burrows are just large enough to allow passage of one spider. Because of this, copulation must occur at the burrow entrance where the female can position herself over the turret thereby making room for the male to adopt a position face down in the burrow. Except for the vertical position,

copulation is typical of that described for other lycosids (e.g., Rovner 1974). Copulation typically lasts over an hour ($\bar{x} = 1.6$ h, SD $= 0.25$, $n = 10$).

Male mating success and mate finding.—All males that were offered a second female proceeded through normal courtship. In every case, once-mated female *Geolycosa* rejected a second male regardless of previous experience with that male. Rejection behavior involved repeated attacks by the female during the male approach. Fewer than five such attacks ($\bar{x} = 4.2$, SD $= 1.1$, $n = 45$, n refers to the total number of female attacks observed) were sufficient to cause the male to cease further attempts.

When previously mated males were offered females without burrows, empty burrows of mature females, or turret material, they engaged in orientation behavior and proceeded with an approach. Males courting females without burrows proceeded through a normal approach and into the contact phase. These males were eventually rejected by the females.

Males exposed to the empty burrows of mature females engaged in normal approaches followed by foreleg searches of the empty burrow (see description above). Such males made several probes. Males courting turret material made normal approaches and engaged in leg tapping of the material.

DISCUSSION

The mechanism by which the mature male *G. turricola* finds the penultimate female is unknown (Miller and Miller 1986). However, given the stationary position of the female and the relatively wide spacing of burrows in some *Geolycosa* populations (pers. obs.), one possibility is that long range attraction of the male is mediated by aerial pheromones given off by the immature female. The existence of aerial attractants has been predicted for burrow dwelling spiders (Robinson 1982).

The use of draglines for attracting males from a distance (Tietjen 1977) seems unlikely. *Geolycosa* rarely wander more than a few cm from their burrows, even during foraging (pers. obs.). We also presently have little evidence that immature female *Geolycosa* produce percussive or stridulatory sounds to attract mature males, although further investigation in this area is needed.

Certain components of the courtship of *G. turricola* are similar to those described for other lycosids. The foreleg-high approach posture of the males is similar to the courtship posture of mature male *Lycosa carolinensis* Walckenaer (Farley and Shear 1973; pers. obs.) and *L. malitiosa* Tullgren (Costa 1975). Leg-waving and leg-tapping has been observed in male *Pardosa* (e.g., Den Hollander and Dijkstra 1974; Koomans et al. 1974), *Schizocosa* (e.g., Uetz and Denterlein 1979) and *Lycosa* (Rovner 1968). Palpal-drumming by the male is similar in form to that described for other lycosids (e.g., *L. rabida* Walckenaer, Rovner 1968).

However, *G. turricola* courtship differs from the typical lycosid pattern (Robinson 1982) in the absence of pronounced abdominal vibrations and ritualized palpal movements. Palpal movements may provide visual stimulation of the female (e.g., palpal rotation of *L. rabida*, Rovner 1968), percussive sound (e.g., palpal-drumming of *Schizocosa mccooki* Montgomery, Stratton and Lowrie 1984) or acoustic signals (e.g., sound produced by palpal stridulation, Rovner 1975). Abdominal vibrations may provide vibratory, acoustic or visual signals. Subtle abdominal movements produce substrate vibrations in some spiders

(Rovner and Barth 1981), but the abdomen of male lycosids does not generally touch the substrate during vibrations (Rovner 1968, pers. obs.). Acoustic sounds are not likely in *G. turricola* since abdomen-prosoma type stridulatory organs (Legendre's type a, 1963) are not known for lycosids (Uetz and Stratton 1982). Although the abdomen of the male *G. turricola* is probably visable to the female during the male's tiptoe display, we observed no significant movements of the abdomen during that time.

A reduction of the visual component of courtship (non-sound producing palpal movements and abdominal vibrations) may reflect the relatively greater importance of chemotactic communication during cohabitation over visual courtship signaling by the male. There is evidence that visual signals are not as important in lycosid courtship as chemotactic, vibratory and acoustic signals. Wolf spiders are thought to have poor visual acuity (Homann 1931), and the experimental removal of the palps of courting male *L. rabida*, and, thus, the removal of the palpal rotation display, did not prevent the mating success of the male under laboratory conditions (Rovner 1968). Cohabitating male *Geolycosa* position themselves face down in the burrow and, in order for courtship to proceed, must exit the tunnel (Miller and Miller 1986). Our observations indicate that the male is, in fact, gently pushed from the burrow by the mature female. This close contact between the mature male and female provides a pre-courtship opportunity for the male to stimulate the female and, thus, may lead to a less elaborate courtship, such as we observe here. However, pre-courtship contact alone may not negate the necessity of visual display. Some lycosids (e.g., *L. helluo* Walckenaer, Nappi 1965; *S. mccooki*, Stratton and Lowrie 1984) require contact between male and female to initiate courtship but still engage in fairly elaborate visual display, and we show here that *G. turricola* males signal vigorously with their palps in some situations during courtship. Further, the presence of distinctive epigamic coloration on the distal foreleg segments of most *Geolycosa* (Wallace 1942) suggests some importance of visual display in these spiders. The possible significance of the less well-developed visual display in *G. turricola* requires experimental studies.

Our results indicate that female *G. turricola* are obstructed in their view of the approaching male until he is very close to the burrow. Although this may contribute to the relative unimportance of visual display on the part of the male, it might also suggest a greater emphasis on vibration or sound production and chemical signaling. With regard to sound production in burrowing spiders for example, ctenizid males that are approaching the burrows of mature females drum the ground with their first pair of legs (Buchli 1969). However, our observations suggest that vibratory and airborne sounds are not important in *Geolycosa* courtship. We believe that the lack of such sounds is to a large extent mitigated by chemical signaling during cohabitation and courtship. However, as we mentioned earlier, the possibility of vibration or sound production in these spiders needs further investigation.

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