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COURTSHIP AND COPULATORY BEHAVIOR OF THE FUNNEL-WEB SPIDER, *HOLOLENA ADNEXA* (ARANEAE, AGELENIDAE)

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ABSTRACT

Courtship and copulatory behavior were observed in the funnel-web spider, *Hololena adnexa* (Chamberlin and Gertsch). Overall these behaviors were similar to those reported for *Agelenopsis* species. However, behavioral differences were found in the precopulation stage.

An unusual pattern for male palpal insertion duration during copulation was discovered. Initial short duration insertions were followed by a peak of longer insertion durations; however, subsequent insertions decreased in duration. The peak in insertion duration was postulated to correspond to the maximum time of transfer of sperm.

INTRODUCTION

Basic life history data have yet to be gathered for many spider species, and this deficiency is particularly noticeable in the areas of courtship and mating behavior (see recent review by Robinson 1982). In the family Agelenidae there have been a few studies and these are briefly reviewed. Gering (1953) focused on courtship and copulation in three species of *Agelenopsis: A. aperta* Gertsch, *A. oklahoma* Gertsch, and *A. pennsylvanica* C. L. Koch. He also presented a detailed description of the mechanics of palpal insertion for these species. Krafft et al. (1978) recorded the frequency of vibratory signals produced by male *Tegenaria parietina* (Fourcroy) and *Coelotes terrestris* (Wider) during courtship. Leborgne et al. (1980) examined the possibility that males use chemical cues to recognize female webs and recorded the frequency of vibrations produced by males during courtship for *Tegenaria domestica* (Clerck) and *T. pagana* C. L. Koch. Using these same species and *Coelotes terrestris*, Roland (1984) found males orienting to draglines of conspecific females in T-maze experiments.

The current study focuses on the courtship and copulatory behavior of a western U.S. agelenid, *Hololena adnexa* (Chamberlin and Gertsch). *Hololena adnexa* is one of the most common urban garden spiders in the San Francisco Bay Area of California, yet like many spider species it has received no more than casual attention to date. It builds a typical horizontal agelenid non-sticky web with a funnel retreat on shrubs, trees and more rarely on the ground in plant duff. Often, large numbers of these spiders can be seen covering shrubbery with their dense webs. They become most noticeable in late summer, when one web can cover an area 20 cm or more in diameter. *Hololena adnexa* served as a good study animal since it was abundant and was maintained readily under laboratory conditions.

METHODS

Penultimate male and female *Hololena adnexa* were collected from landscape shrubs in Berkeley, California in the fall of 1980. They were kept in 97 mm × 27 mm glass vials plugged with cotton. House flies were provided as prey once a week, but no free water was given since previous rearings showed that it was unnecessary.

Virgin individuals were placed in separate plastic boxes (6.0 cm × 10.2 cm × 10.2 cm) 2 weeks prior to mating observations. For each mating, a male was placed on the edge of the female's web. Mating observations were made with and without the aid of a dissecting microscope. Insertions of each palpus were counted and timed. At the end of each mating the male was removed and the female was allowed to construct egg sacs within the box. Only those matings that resulted in fertile eggs were considered valid. Means are followed by standard deviations throughout this paper.

RESULTS

During the six-month period of study, seventeen complete matings were observed for 17 females and 14 males of *H. adnexa*. They constituted the basis for a five-step mating sequence (adopted from Gering (1953)) reported below.

Step 1-Courtship.—When placed on the female's web, the male responded by vigorously pumping his legs and abdomen in the vertical plane without palpal drumming. This produced one to six bouts of vibration, with each lasting from 3 to 90 sec. How often this behavior occurred was a function of the female's actions. In response to the male's movement on the web, the female usually went into cataleptic paralysis, characterized by drawing the legs close to the body and remaining immobile, as reported by Gering (1953). When the female became cataleptic after the initial vibrations, the male continued vibrating and searching until he found her. In two instances, she did not recognize the male after these first vibrations and attacked him as if he were prey. The male repelled such attacks with his longer legs, and a few additional vibrations caused the female to become cataleptic.

Step 2-Precopulation.—When the male found the female, usually in the funnel portion of the web, he grasped her last two pairs of legs in his chelicerae, near the patellae, facing the female's caudal end. He then lifted and dragged her to a different portion of the funnel. The time interval between male placement on a web and location of the female averaged 32.8 ± 20.3 min. This step ended when the male stopped moving, momentarily released the female, and turned her on her side in preparation for copulation. The length of time from first contact with the female to initiation of copulation averaged 9.8 ± 11.8 min.

Step 3-Copulation.—The male began copulation by moistening both palpi, drawing them one at a time through his chelicerae. He then applied either the right or left palpus to the female's epigynum, depending on which side she lay. If on her right side, he applied the right palpus; if on her left side, the left palpus (Fig. 1). Successful insertion of the embolus was outwardly evidenced by a noticeable swelling of the hematochae of that palpus. The number of repeated insertions of one palpus was variable among the test spiders, averaging 81.8 ± 25.6. However, duration of insertions followed a regular pattern (Fig. 2). For

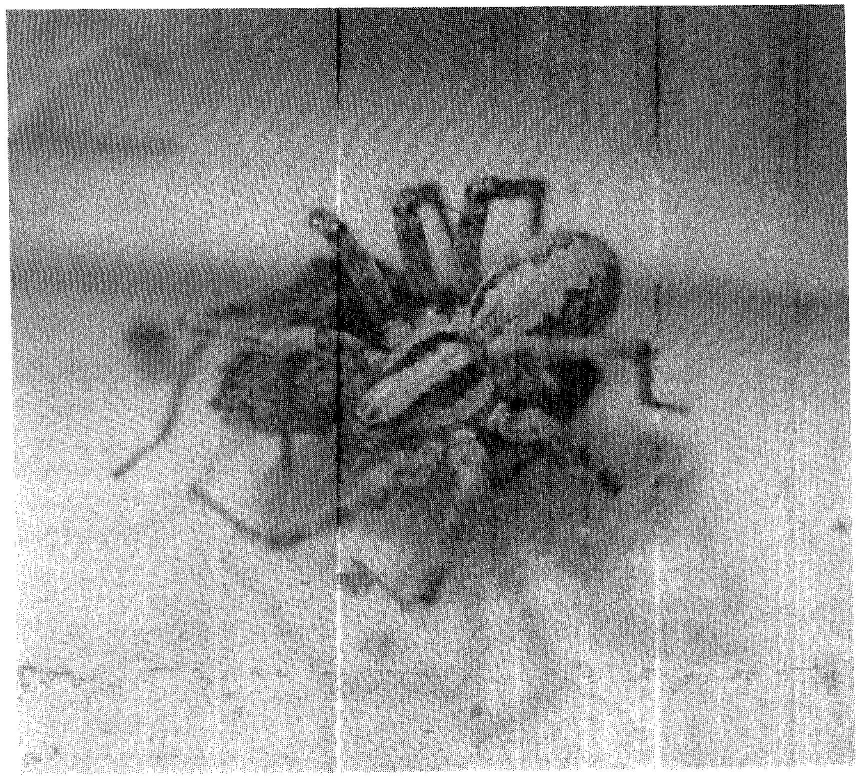

Fig. 1.—Male and female in mating position.

approximately the first 20 insertions the hematochae became inflated for several seconds; subsequent insertions lasted 1 to 2 min. These longer insertion times continued for several palpal applications, but gradually diminished. After the male finished inserting one palpus he grasped the female and moved her to a new location before proceeding with the unused palpus. Only infrequently did the male turn the female on her other side and begin applying the other palpus. Occasionally a male experienced difficulty in keeping the embolus inserted when inflating the genital bulb. If this occurred, he cleaned the embolus and attempted the insertion again, sometimes up to 10 to 15 times. If still unsuccessful, he turned the female on her sternum and moved her to a new location or just turned her on her side and tried again, either with the same or the other palpus. During most matings each palpus was used in a single long series of insertions. However, in three cases, in which both palpi had already been used in a mating, the males reverted back to using the original palpus. The timing of these insertions did not follow the pattern for the initial insertion series, since no distinct maximum insertion time occurred (Fig. 3).

Step 4-Postcopulation.—Following copulation, the male groomed his palpi and walked off and away from the female, leaving her in a cataleptic state for several seconds. Only twice when the male walked away did the female quickly recover and chase him off the web. Time from male placement on the web to departure from the mated female averaged 166.1 ± 43.1 min.

Step 5-Sperm induction.—After each mating, the male was placed in a vial, where he soon refilled his palpi with sperm. I saw this behavior only three times

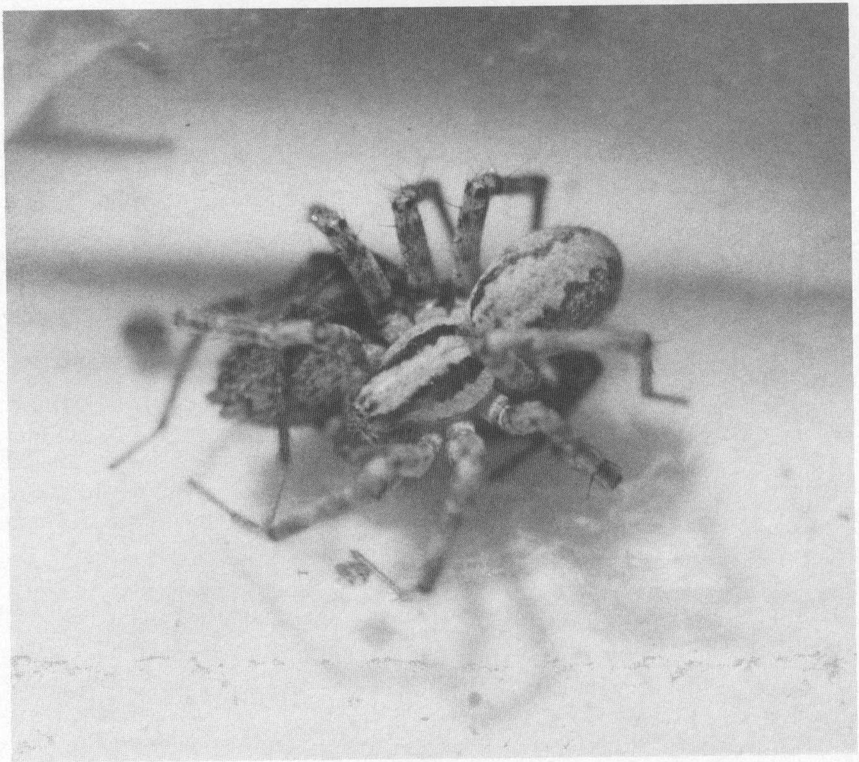

Fig. 1.—Male and female in mating position.

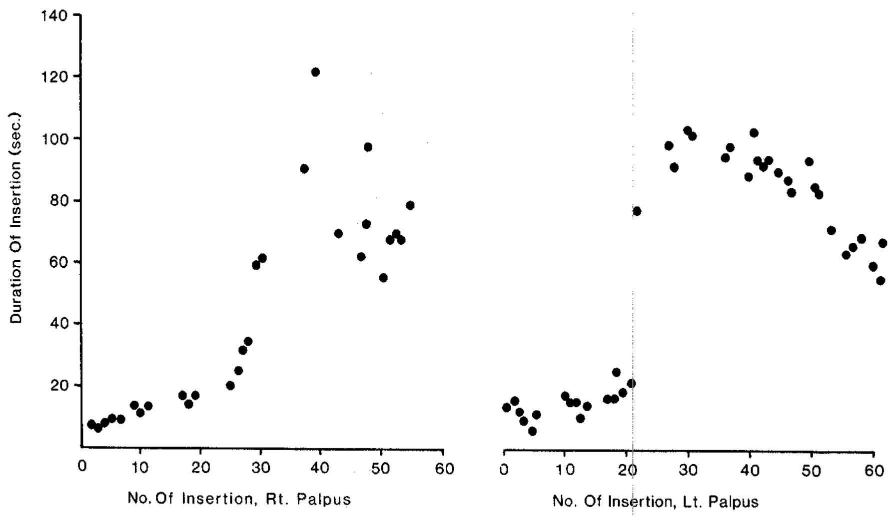

Fig. 2.—Relationship between duration and sequence of insertions of the right and left palpi of a single representative mating of *Hololena adnexa*.

and never completely for one spider; however, a general summary of the activity is offered. Sperm induction begins with the male spinning a small rectangular "sperm" web, which is broader at the ends than the middle. A drop of sperm from the genital aperture is placed on the center of the web. The male centers his cephalothorax over the web, moistens his palpi, and alternately applies each palpus to the sperm droplet by reaching beneath the web. During this procedure no evidence of hematochal swelling can be observed. The entire process of web building to charging of palpi lasts 25 to 30 min.

DISCUSSION

Male chemotactile perception of a pheromone on conspecific female silk has been demonstrated in at least four web-building spider families; Araneidae, Linyphiidae, Theridiidae, and Agelenidae (Meyer 1928; Suter and Renkes 1982; Ross and Smith 1979; Leborgne et al. 1980). Initiation of mating behavior in *H. adnexa* males occurred when the male touched female silk. This suggests either a chemotactic or tactile stimulus. Visual cues were unlikely, for when courtship was initiated the female was in the funnel of the web and not visible. Chemical, tactile, or both types of cues from the webs of *H. adnexa* females probably trigger courtship behavior in males. Chemotactic reception during courtship has been implicated previously in three other agelenids: *Tegenaria domestica, T. pagana* and *Coeletes terrestris* (Leborgne et al. 1980; Roland 1984).

Successful copulation is dependent on the coupling of the male palpus to the female's epigynum. Gering (1953) provides great detail on how the male palpus of *Agelenopsis* mechanically fits into the female epigynum. Probably the most critical structure is the conductor of the palpus, which locks into a coupling cavity anchoring the palpus onto the epigynum. This allows the genital bulb to twist the embolus into the female's bursa. Gering examined male and female structures of an unidentified species of *Hololena* and found them capable of the same procedures described for *Agelenopsis* mating.

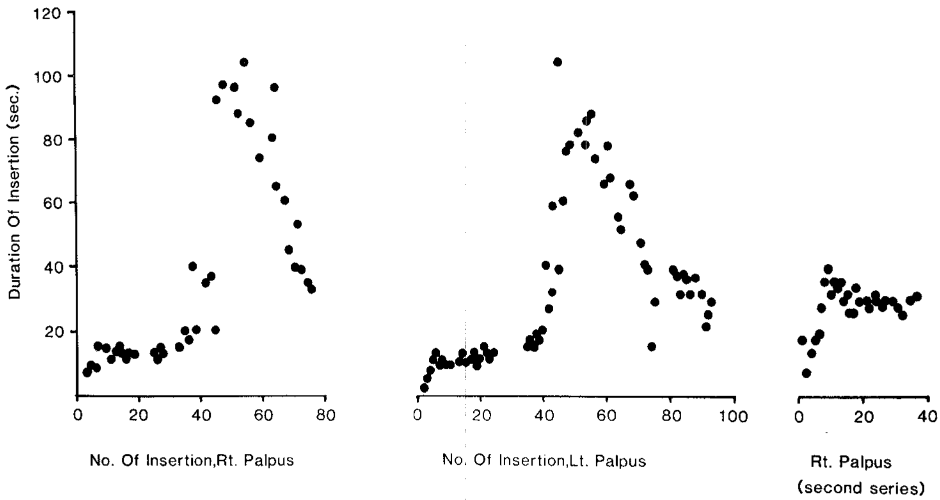

Fig. 3.—Relationship between duration and sequence of insertions of the right and left palpi of a single representative mating of *Hololena adnexa* with a second series for the right palpus.

Positioning of the female by the male is critical for successful copulation, aligning male and female structures for a proper fit. Alignment of male to female takes place during the precopulation stage. Gering (1953) divided this stage into four substages: contact, reversal, positioning, and cleaning. Differences were observed in the first three substages between *H. adnexa* and *Agelenopsis*. Gering described the contact stage as a lunge and quick seizure of the female, a behavior not observed in the male of *H. adnexa*, which slowly touched and grasped the female. After grasping her, the male usually moved her to another location in the funnel, a behavior not reported for *Agelenopsis*. Gering stated that mounting the female usually occurred from the rear, making reversal necessary. In all but a few of the *H. adnexa* matings, mountings were from the front, thereby eliminating the need to reverse position. The positioning substage in *Agelenopsis* and *H. adnexa* was quite different. In *Agelenopsis*, the male is draped across the female at an angle of 45^0, while the male *H. adnexa* stood parallel alongside the female. The differences found in the mating stance between *H. adnexa* and *Agelenopsis* may relate to differences in structure of the male palpi.

A pattern for palpal insertion duration was found for *H. adnexa* that has not yet been described in agelenids. Gering did not follow a complete mating between male and female *Agelenopsis*, since he interrupted mating after six insertions and concentrated on the timing and mechanics of individual insertions. Therefore, Gering could not have observed how insertion times may have changed during a mating. In *H. adnexa* insertion durations were found to be shorter at the beginning and end of a series than halfway through it (Figs. 2 and 3). The longest insertion lasted about 100 sec. I hypothesized that all short interval insertions (20 sec or less) previous to this peak probably resulted in no sperm transfer. Maximum distension of the hematodocha for *Agelenopsis* species was equated with transfer of sperm, and this required an average of 72 sec and a minimum of 16 sec. Although the amount of time required for maximum distension in *H. adnexa* is unknown, it may be that an insertion lasting 20 sec or less would not allow enough time to totally insert the embolus, based on the similarity of palpal morphology to *Agelenopsis* species.

The duration of insertion at maximum distension may be determined by the quantity of sperm transferred. Maximum insertion time would then represent the period when maximum transfer of sperm occurred. Insertions immediately following the insertion time peak could serve to deplete what sperm remained in the fundus. When males were observed reinserting a palpus in a second series, this could also be for emptying any remaining sperm. Depleting the fundus may account for there not being a peak for the second series, but just a number of insertions for approximately equal time intervals (all longer than 20 sec) (Fig. 3).

An alternate interpretation presented first by Helsdingen (1965) for *Lepthyphantes leprosus* (Ohlert) and subsequently tested by Rovner (1975) on *Schizocosa saltatrix* (Hentz) and *S. avida* (Walckenaer) states that a structure associated with haematodochal inflation, for instance a valve within the palp, becomes fatigued with repeated use during copulation. Thus, insertion durations increase during copulation.

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