

COURTSHIP BEHAVIOR AND SEXUAL CANNIBALISM IN THE SEMI-AQUATIC FISHING SPIDER, *DOLOMEDES FIMBRIATUS* (CLERCK) (ARANEAE: PISAURIDAE)

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ABSTRACT. The courtship behavior of the semi-aquatic Pisaurid fishing spider *Dolomedes fimbriatus* was examined in the laboratory. Male courtship was triggered by the presence of female drag-lines, presumably by a female sex pheromone since males did not respond with courtship to male drag-lines. Male courtship behavior included vibratory signaling (water surface waves), leg-waving, and following female drag-lines. Vibratory signaling was a major courtship component, and signals were produced at a regular rate (mean rate: 8.33 ± 1.53 s, $n = 97$). Irrespective of whether females were mated or unmated, females were very aggressive towards males, and sexual cannibalism prior to copulation occurred in 6.6% of the female attacks on males ($n = 76$). The capture success rate of females depended on whether the male was attacked from a distance or from immediate proximity. The occurrence of sexual cannibalism of courting males by virgin *Dolomedes* females is discussed, and it is suggested that this behavior of fishing spiders may represent an adaptive female strategy rather than mistaken identity.

The semi-aquatic fishing spiders of the genus *Dolomedes* (Pisauridae) are large spiders that inhabit various freshwater habitats such as the shoreline of streams and lakes (Carico 1973). The main prey of fishing spiders are other aquatic and semi-aquatic invertebrates and vertebrates, and terrestrial invertebrates trapped at the water surface (Bleckmann & Lotz 1987; Zimmermann & Spence 1989). The sensory ecology of fishing spiders with regards to predation has been rather well examined (Carico 1973; Williams 1979; Roland & Rovner 1983; Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann 1985). In contrast, the reproductive behavior of fishing spiders has been thoroughly described only for the Nearctic species *D. triton*, where vibratory, tactile, chemical, and visual communication all play important roles during courtship (Roland & Rovner 1983; Bleckmann & Bender 1987). Such information of the Holarctic species *D. fimbriatus* is limited, and only scattered observations in older studies are available (Pappenheim 1903; Gerhardt 1926; Schmidt 1953, 1957).

The purpose of the current study is to describe male courtship behavior as well as female response to male courtship in *D. fimbriatus*, and to evaluate the relative roles of vibratory, tactile, chemical, and visual stimuli during courtship. *Dolomedes* spiders are known to exhibit sexual cannibalism (females killing and consuming males) (Schmidt 1957; Zimmermann & Spence

1989; Foelix 1982; Elgar 1992), and the occurrence of sexual cannibalism in *D. fimbriatus* is quantified and discussed.

METHODS

Adult *D. fimbriatus* were collected from a dense population at Sirapsbacken (64° 22' N, 19° 28' E), an alluvial meadow by the river Vindelälven in northern Sweden. A total of 25 females and 17 males was captured on June 17-18, 1991. Individuals were placed individually in plastic aquaria (0.45 × 0.25 m) filled with water to a depth of 8 cm. Each aquarium was provided with three pieces of floating styrox elements (15 × 5 cm) which served as resting sites. Ambient temperature was 20 °C ± 1 °C, and males were fed daily one water strider (*Gerris odontogaster*) per individual. Females were fed one water strider and one field cricket (*Gryllus bimaculatus*, > 20 mm body length) per individual per day.

Behavioral observations were made in trials, where one male was introduced to a female in her aquarium for 50 minutes. When introduced, males were carefully placed at the water surface as far away from the female as possible, on the opposite side of the aquaria. During each trial, the behavior of the spiders was observed visually and videotaped for subsequent behavioral analyses from slow motion replays. A total of 36 trials was performed. In a first round of trials ($n = 25$), all females were exposed to a male. In a second

round ($n = 11$), all females that had not yet laid eggs were allowed a second exposure to a male. Males were numbered individually and used for behavioral trials in numerical order. Thus individuals were chosen systematically for the behavioral trials, and each female was used 1–2 times and each male 2–3 times (if not eaten by a female in the first round). After the behavioral trials, females were fed (see above) and allowed to lay and tend their eggs. Ten days after the date of egg laying, the egg sac was opened. By this time the embryos in fertilized eggs were clearly visible, and the fertilization rate of the egg batch could thus be recorded.

In order to determine the role of chemical stimuli relative to that of visual and tactile in triggering male courtship behavior, a series of experiments was performed. In addition to the behavioral trials described above (treatment I, $n = 36$), males were also introduced (in numerical/systematical order by being carefully placed at the water surface) into one of three types of aquaria: male aquarium with a male (treatment II, $n = 5$), uninhabited new and thus clean aquarium with a styrox element from a female aquarium (treatment III, $n = 6$), and uninhabited new and clean aquarium with a styrox element from a male aquarium (treatment IV, $n = 5$). The styrox in treatments III and IV was covered with drag-lines from their previous environment. In each of these trials (treatments II–IV), the spiders were observed for 50 minutes, and it was recorded only whether or not the introduced male exhibited courtship.

RESULTS

Of the 25 females brought to the laboratory, 17 were penultimates (performed their ultimate moult in the laboratory prior to the behavioral trials) and eight were adults. Seventeen females were thus virgin, whereas the mating status of the females collected as adults was unknown at the time of the behavioral trials. However, the mating status of these females could be determined after the experiments since unmated *D. fimbriatus* females eat their unfertilized eggs after egg deposition (Schmidt 1957), which is also the case in *Pardosa* wolf spiders (Lycosidae) (Vlijm et al. 1963; Kessler 1970). After the behavioral trials, 16 females laid unfertilized eggs that were partially consumed by the female (15 collected as penultimates and one collected as adult). Nine females laid and tended their eggs (two collected as penultimates and seven as adults). In five cases

the egg batches were incompletely fertilized (fertilization rate 25–50%) and in four cases the egg batches were completely fertilized (fertilization rate > 95%). Females that tended their egg sac laid 350.8 ± 79.4 eggs per egg sac ($n = 9$).

Courtship.—When a male *D. fimbriatus* was introduced into an aquarium inhabited by an adult female (treatment I), the initial male response was an “announcement display”. This behavior commenced on average 3.09 ± 3.21 min ($n = 36$) after introduction to the aquarium, apparently always when the male first made physical contact with a female drag-line (irrespective of whether the drag-line was placed on the water surface or on a styrox element). The announcement display consisted of two major components; vibratory signals and leg-waving. Males produced vibratory signals on both substrate types, by a slight elevation of the body followed by a sudden jerky lowering of the abdomen, causing concentric water surface waves to spread out from the male (when vibratory signals were performed at the water surface). These jerks were made in the same manner as in *D. triton* males (Bleckmann & Bender 1987). Vibratory signals were produced at a regular rate, once every 8.33 ± 1.53 s ($n = 97$), and males often continued to produce vibratory signals throughout the trials (50 min). During the inter-vibrational pauses, males occasionally performed leg-waving, where the spider lifted and waved legs I. When leg-waving, the male alternated between the left and right leg in an irregular vertical waving-pattern with the legs typically being held extended forward, straight and stiff. Leg-waving was often combined with a rapid tapping with legs I on the substratum, especially when on styrox, presumably producing additional vibrations. When placed in a female aquarium males moved very slowly, typically a few mm/min, normally following a female drag-line with the palps and legs I. Vibratory signals, leg-waving, leg-tapping, and very cautious advance along a female drag-line during the inter-vibrational pauses were alternated. Males performed announcement display for 29.36 ± 14.71 min ($n = 36$) during each trial.

Males seemed unable to visually detect motionless females, for males frequently (1.42 ± 0.39 times per trial) passed in very close range (nearest distance between tips of legs less than 2 cm) behind them, apparently without detecting their exact location.

The role of chemical stimuli.—Males always

responded with courtship when placed in a female environment (treatments I and III), but never exhibited courtship in male environment (treatments II and IV) ($\chi^2 = 53.0$, $df = 3$, $P < 0.001$; Table 1). In treatment III, males typically commenced with courtship signaling upon first physical contact with a styrox element from a female cage. Males did not respond to drag-lines of other males (treatment IV).

Female response to male courtship.—Females typically remained motionless during the behavioral trials with legs III and IV anchored to styrox and the anterior two pairs of legs resting upon the water surface, and no female courtship was observed. However, the females exhibited two different responses to male courtship which will be described below; attack from a distance and passivity. A total of 89 male-female interactions was observed. The first interaction in a trial occurred after 26.6 ± 19.7 min ($n = 36$), and 76% of the interactions consisted of female attacks on males from a distance. The average attack distance was 6.76 ± 3.53 cm ($n = 26$). In 97% of these long distance attacks males avoided capture by rapid evasive movements, often including a change of direction (approximately 90°) making it more difficult for females to pursue males. In three of these cases, the males were seized by the females but escaped by rapidly autotomizing legs. However, in the other 3% of the attacks, males were caught and cannibalized by females.

In 24% of the interactions, females remained passive when the male approached. Males making physical contact with a female immediately started to tap vigorously with legs I and II on her legs and abdomen for 2.03 ± 1.42 min, after which the male immediately mounted the female from behind and attempted copulation. When mounting, males climbed up onto the abdomen of the female, turned around (facing in a direction opposite that of the female) and slid somewhat sideways in order to reach the epigynum with its palps. Only two successful copulations occurred. In both cases, only one palp was inserted and the females involved were virgin females collected as penultimates which later laid and tended incompletely fertilized egg batches. Although no data on exact palpal insertion times were collected, they were both very brief (< 15 sec) in accordance with the observations made by Schmidt (1957).

During the phase of physical contact (male on top of female), lasting 1.36 ± 0.83 min, the fe-

Table 1.—The occurrence of male *Dolomedes fimbriatus* courtship behavior in different experimental treatments in the laboratory.

| Treatment | Total no. of trials | No. of trials yielding courtship response |
|------------------------------------------------------------------------|---------------------|-------------------------------------------|
| I. Male introduced to a female in female aquarium | 36 | 36 |
| II. Male introduced to a male in male aquarium | 5 | 0 |
| III. Male introduced to a new aquarium with styrox element from female | 6 | 6 |
| IV. Male introduced to a new aquarium with styrox element from male | 5 | 0 |

male either remained totally passive (62% of the cases) in which case the male attempted copulation and then made a sudden vertical jump followed by rapid withdrawal, or females suddenly attacked the male (38% of the cases). When attacking a male in physical contact, females caught and cannibalized males in 37.5% of the cases, a success rate significantly higher than long distance attacks (Fisher exact contingency table test [two-tailed], $P = 0.016$). In total (for both types of attacks, $n = 76$), males were caught and cannibalized in 6.6% of the attacks.

There were no apparent differences in response to male courtship between mated and unmated (virgin) females, and females did not differ significantly in level of aggression; females attacked the male in 73.1% of the interactions involving mated females ($n = 26$) and in 76.2% of the interactions involving unmated females ($n = 63$) (Fisher exact contingency table test [two-tailed], $P = 0.791$).

DISCUSSION

In general, the courtship behavior of *D. fimbriatus* includes many components typical for Pisaurid and Lycosid courtship, such as vibratory signaling, leg-waving, and female drag-line following (Barth 1982; Foelix 1982; Robinson 1982; Tietjen & Rovner 1980, 1982; Roland & Rovner 1983; Bleckmann & Bender 1987). Communication between the sexes in *D. fimbriatus*

during courtship probably relies on vibratory (jerks and leg-tapping on substratum), visual (leg-waving), and chemical stimuli during the initial phase and tactile stimuli (leg-tapping on female) during later phases. This is similar to the courtship behavior of *D. triton*, where vibratory communication has been shown to play a major role during courtship (Roland & Rovner 1983; Bleckmann & Bender 1987). However, while the water surface wave signals of *D. triton* are produced at irregular intervals (Roland & Rovner 1983; Bleckmann & Bender 1987), *D. fimbriatus* produced these signals at a regular rate suggesting that interspecific differences occur in the pattern of signaling. There may be additional differences between the species with regards to signal wave parameters, e.g., frequency content, duration and amplitude (Bleckmann & Bender 1987).

In *D. scriptus* and *D. triton*, male courtship behavior is triggered by chemical stimuli, and visual/vibrational cues are not required (Kaston 1936; Roland & Rovner 1983). The results of the current study show that this is the case also in *D. fimbriatus*, and suggest that the female sex pheromone is bound to the female's drag-line. Distance chemoreception does not seem to occur in *D. fimbriatus* (cf. Tietjen & Rovner 1982).

Several previous studies have demonstrated that *Dolomedes* females may be very aggressive towards courting males, and that sexual cannibalism may occur (Gerhardt 1926; Schmidt 1957; Roland & Rovner 1983). Further, in a field study of *D. triton*, Zimmermann & Spence (1989) showed that one of the most important prey items of adult female fishing spiders was adult males, confirming that sexual cannibalism in natural populations is an important phenomenon in this group of spiders. *D. fimbriatus* females in the current study were extremely aggressive towards males, and female mating status did not affect the level of aggression. Despite vigorous courtship, males were usually attacked even when approaching virgin or incompletely mated females in most cases, and several instances of sexual cannibalism occurred. It is further worth noting that females had a significantly higher attack success rate when attacking males in immediate proximity compared to attacks from a distance.

There is a current controversy over the evolution of sexual cannibalism (Buskirk et al. 1984; Gould 1984; Elgar 1992). Sexual cannibalism after copulation may represent an adaptive male paternal investment strategy (Thornhill 1976; Buskirk et al. 1984), while sexual cannibalism

prior to copulation may be adaptive even for virgin females (Elgar 1991; Newman & Elgar 1991). Sexual cannibalism may also simply represent cases of "mistaken identity" (Robinson 1982; Elgar 1992). *Dolomedes* females may be characterized as sit-and-wait predators. The posterior legs are normally anchored to a firm object (e.g., a rock or the vegetation), while the anterior legs are spread out on the water surface (Carico 1973; Williams 1979). Studies of the sensory ecology of fishing spiders have demonstrated that females in this typical position have a sophisticated system for detecting and interpreting water surface wave vibrations, and that females are capable of discriminating prey and non-prey generated surface waves (Williams 1979; Roland & Rovner 1983; Bleckmann & Barth 1984; Bleckmann & Rovner 1984; Bleckmann 1985). In a study of the vibratory component of courtship, Bleckmann & Bender (1987) concluded that the courtship surface wave signals of male fishing spiders are insufficient to release female prey capture behavior since they lack prey wave characteristics, and that females should be able to identify males solely on the basis on vibratory cues. This conclusion, combined with the fact that sexual cannibalism in fishing spiders occurs primarily before copulation (Gerhardt 1926; Schmidt 1957; Roland & Rovner 1983; this study), suggests that cannibalism of courting males by virgin fishing spider females might represent an adaptive female strategy rather than cases of mistaken identity. Virgin *D. fimbriatus* females may benefit from killing and consuming a courting male provided that the risk of remaining unmated is low (see Newman & Elgar 1991). However, it is difficult to distinguish between different models of sexual cannibalism, and future work should be directed at testing the various assumptions and predictions of the model of Newman & Elgar (1991).

ACKNOWLEDGMENTS

Thanks are due to C. Otto for constructive comments on the manuscript, and to S. Diehl for providing assistance with the experiments.

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Manuscript received 25 May 1992, revised 11 September 1992.