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SEXUAL BEHAVIOR IN *DICTYNA VOLUCRIPES* (ARANEAE, DICTYNIDAE)[1]

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ABSTRACT

Courtship and mating in *Dictyna volucripes* Keys. are described on the basis of laboratory observations of 13 virgin pairs. Their behavior conformed well to the general pattern within the family. Various features of both female and male behavior are consistent with the view that courtship functions mainly in influencing mate-choice by females, rather than in inhibiting predatory attack upon males.

Laboratory and field observations show that pairs commonly remain together for some days after mating. While the function of such cohabitation is unknown, it can evidently provide an important preadaptation in the evolution of spider sociality.

INTRODUCTION

The Dictynidae is a widespread family of small to medium-sized, cribellate spiders which make irregular webs. In recent years much attention has focused on the permanently social *Mallos gregalis* (Simon), which has in turn called comparative attention to the behavior of more typically solitary or intermediate species (Honjo 1977; Jackson 1977-1979; Uetz 1983).

Observations of courtship and mating have been reported from about 12 species of Dictynidae (Karpinski 1882; Montgomery 1903; Berland 1916; Gerhardt 1924; Locket 1926; Billaudelle 1957; Leech 1966; Bristowe 1971; Jackson 1979). Before Jackson's (1979) analysis of sexual behavior in two *Mallos* species and *Dictyna calcarata* Banks, observation was mostly rather superficial, with few quantitative data. As a result, comparisons based on the older literature are often inconclusive.

Jackson (1979) has reviewed sexual behavior in the family. In this paper I describe courtship and mating in an additional species, with some remarks on post-mating cohabitation.

Dictyna volucripes Keys. is widespread in eastern North America (Chamberlin and Gertsch 1958) and often locally abundant. In eastern Kansas I have found the web typically in the upper part of a small plant, where it forms an irregular tent over a flowerhead or several twigs. A small region of the interior is

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[1] Contribution no. 1974 from the Department of Entomology, University of Kansas, Lawrence, Kansas 66045. This paper is dedicated to Willis J. Gertsch on the occasion of his 80th birthday, 4 October 1986. Dr. Gertsch has been very generous to me and many other amateur arachnologists.

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Fig. 1.—Part of a *D. volucripes* web with a mating pair in the retreat area. The opening to the retreat is in the middle foreground.

reinforced with silk to form a distinct, tubular retreat (Fig. 1). The spider is most often found motionless within the retreat. For a clear illustration of web structure in a related species, see Bristowe (1971: Fig. 41).

Preliminary observations in old fields in eastern Kansas indicate that *D. volucripes* usually overwinters in the subadult stage and that males molt to adulthood a few days before females. Sexual dimorphism is not pronounced, with adult females only slightly larger than males. Scheffer (1905) reported the appearance of egg-sacs in the webs from late June to late September in this area, with 15 eggs/sac and usually 1-5 sacs/web.

MATERIALS AND METHODS

Female and male subadult spiders were collected in northeastern Kansas in March-April of 1975 and 1976. Individuals were reared to adulthood in separate vials, so that all were known to be virgin when first paired. Both as subadults and adults, spiders were provided with flies (*Drosophila* sp.) as prey and appeared well fed, except as otherwise noted. Newly emerged females were introduced onto separate dry, tree-like plant stalks (henceforth called "trees") which simulated wild web-sites and then left to spin webs. Each tree was held upright in sand and covered with a large glass jar, so that it was free on all sides. After 1-3 days, the jar was removed, an adult male introduced at the tree base, and behavior noted with the aid of a tape recorder and hand lens. After a pair had shown no apparent sexual behavior for at least 30 min, we ended observation and replaced the jar. The pair was checked daily for the next four days for a general indication of its condition.

Specimens from Kansas collected and determined by C. K. Starr in 1975-1976 can serve as vouchers. These are deposited in the Snow Entomological Museum at the University of Kansas and the Canadian National Collection in Ottawa.

RESULTS

The following account is based on observation of 13 pairs. In three of these the female had been kept without food for up to two weeks; in all others both partners were well fed. An additional pair which showed no apparent pattern of sexual behavior is disregarded.

Courtship.—At the time of male introduction, the female was usually in the retreat in the **at-rest** posture (Fig. 4): motionless, body lying against the substrate and the legs drawn in close. The male usually began immediately to climb the tree and always reacted strongly upon touching the female's silk. Typically, he walked extensively on the outside of the web, laying down silk. Such **ranging-spinning** was usually rapid and often had a notably agitated appearance. The abdomen twitched up and down, and the pace of walking was very uneven. The palps were held in front, alternately lowered and raised.

The female's first reactions to ranging-spinning could in each case be interpreted as alertness to a potential prey or intruder. She came out of at-rest, extending her legs and raising her body off the substrate. Often she walked out of the retreat, and in some cases rushed toward the male, though without coming very close. As ranging-spinning proceeded, the female showed less and less reaction, and in most cases she entered the retreat and returned to at-rest within a very few minutes.

After several minutes, ranging-spinning gave way to a new phase, **local-spinning**, in which the male walked much more closely around the female and sometimes came to walk directly upon her. In two trials the female moved a short distance away from the male, but in others she remained still. Local-spinning evidently added silk to the retreat, as this came to appear denser. When the male walked upon the female, it appeared from movements of his abdomen that he bound her very lightly with silk.

During both ranging-spinning and local-spinning, males showed little response to female behavior. I could see no reaction when a female simply became alert inside the retreat or walked just outside it. The few times that a female rushed at the male, he retreated on the web, to remain briefly inactive before resuming ranging-spinning. In no case did the female chase a retreating male.

Two trials were performed with a male released at the base of a tree from which the female was newly removed, in order to see his reactions to the web alone. In each case, he went through ranging-spinning and local-spinning as if a female were present.

Local-spinning was followed by a phase in which the pair remained in direct physical contact. In all trials this began with the male coming face to face with the female, their faces apparently touching. This was followed by a period, usually lasting a few minutes, in which the male stroked the female's cephalothorax and parts of her legs with his palps, forelegs, second legs, and occasionally his third legs. As this proceeded, he appeared to attempt to raise her venter away from the substrate with his legs, and in trials which included mating

Fig. 2.—Mating pair of *D. volucripes*.

the **stroking-phase** ended with her rising up. In some trials, this phase was interrupted by a brief return to local-spinning, and in some the female broke contact and moved slightly away, in which case the male local-spun for a time before resuming face-to-face contact and stroking.

Female behavior in the stroking-phase, where she did not break contact, appeared almost entirely passive. She never stroked the male and at most drew her legs in still closer to the body.

Mating.—Raising of the female by the male was always quickly followed by a palpal insertion and was evidently a necessary prelude to it. In three trials without raising there was no insertion, even though in one of these the male courted for more than an hour. In 10 trials with insertion, courtship (comprising the ranging-spinning, local-spinning and stroking phases) lasted for 10-93 min, with a mean of 30 min. In five of nine trials the first insertion was with the left palp, while in four it was the right; in the 10th trial it was not noted.

The mating position in all cases was a variant of Gerhardt and Kaestner's (1937) position I (Figs. 2-3). The male's face was toward the female's sternum, so that the two bodies formed an approximately right angle. The male was rotated to one side, so that one palp was closer than the other to her epigynum, and this palp was inserted. The period of first continuous insertion was very variable, lasting 1-109 min (mean = 56 min, SD = 36 min).

During mating, the hematodocha of the palp pulsated rhythmically. Most of the time it was dilated, with very brief, strong contractions at intervals. In 15 insertions in which a sample of pulsations was timed, the mean interval between contractions was 6.7 s (range = 2-12 s, SD = 2.2 s), with most samples in the 7-9 s range. One male showed an unusual pattern of pulsations during two insertions: after a series of regular, brief contractions, the hematodocha remained contracted for several seconds before the next series of regular contractions.

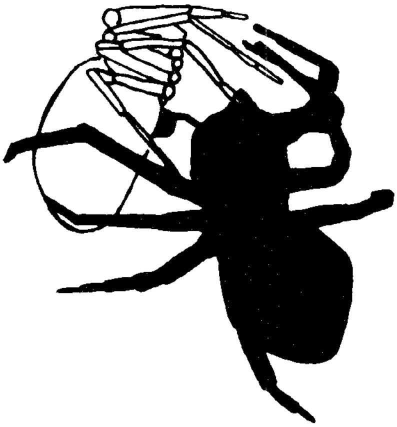

Fig. 3.—Drawing based on Fig. 2. Female in white, male in black.

Further courtship and mating.—At the end of the first insertion phase, the pair disengaged simply and directly. Subsequent behavior was less predictable than that leading up to insertion. The observed variants can be divided into four groups:

a. *No sexual activity.* In two trials the pair soon became motionless and remained so for the rest of the observation period. This was also the usual pattern following final insertion in the next two variants, the pair remaining at rest in or near the retreat (Fig. 4). One of the two pairs was noticed mating again the next day.

b. *Courtship without mating.* In two trials the male resumed local-spinning for a short time, though without subsequent stroking. Courtship in these cases seemed weak and progressively disorganized.

c. *Courtship with mating.* In three trials resumed courtship culminated in insertion of the other palp. In one of these, ranging-spinning preceded local-spinning and stroking. Respective durations of courtship were 12, 25 and 32 min. In the latter the female seemed resistant, as the male made several apparent attempts to raise her before he succeeded. In another of these trials the male again inserted the first palp almost immediately after his second withdrawal, without a return to courtship.

d. *Mating without courtship.* In the remaining three trials the male inserted the second palp without a prior return to courtship. The intervening period was at most about 4 min. In one of these trials the spiders then remained at rest for 79 min, after which the male again inserted the first palp, and almost immediately upon withdrawing it he again inserted the second palp. Another trial was marked by extreme brevity in both insertions and apparent strong unreceptivity of the female after the second withdrawal. It was unclear which partner actively broke contact, but immediately after the first withdrawal the male briefly and unsuccessfully attempted to re-insert the same palp. After the second withdrawal he courted intermittently but vigorously for more than an hour, without further mating that day.

The eight recorded second and subsequent insertions had durations of 4-60 min (mean = 31 min, SD = 23 min). If we disregard the (apparently anomalous) one-minute first insertion, these eight later insertions are significantly shorter (*t*-test, $P < 0.05$).

Fig. 4.—*D. volucripes* pair at rest in web after mating. Female above, male below.

Cohabitation.—We made no systematic observations on the tendency of females and males to occupy webs together, but there are indications that they may commonly do this for extended periods. In the laboratory, pairs left undisturbed after mating remained without apparent conflict during the four days of observation, much of the time together in the retreat. Although the spiders were confined within the glass jar, either could have moved out of the tree and web. In the field later in the season I have often found an adult male in the web together with a female and her egg-cases.

It is also not rare to find more than two spiders in a web. A casual search of perhaps 30-40 occupied webs during two days in April 1976 showed six of them each with three spiders: four with a female and two males, two with two females and a male.

DISCUSSION

Comparison of sexual behavior in *Dictyna volucripes* with what is known from other dictynids shows this species to be quite generalized for the family. Its pattern of courtship and mating is especially close to that described by Billaudelle (1957) from *D. civica* (H. Luc.). Each of the behaviors recorded from *D. volucripes* appears to occur in at least one other species. Among the generalized features of *D. volucripes* sexual behavior are: twitching of the male's abdomen during spinning, face-to-face approach and stroking, mating position I, insertion of one palp at a time, alternation of palps in subsequent insertions, tendency to remain together for some days after mating, and the overall lack of aggression within the pair. I have assumed that abdominal twitching and face-to-face contact are each homologous in different species, though Jackson (1979) noted differences in form.

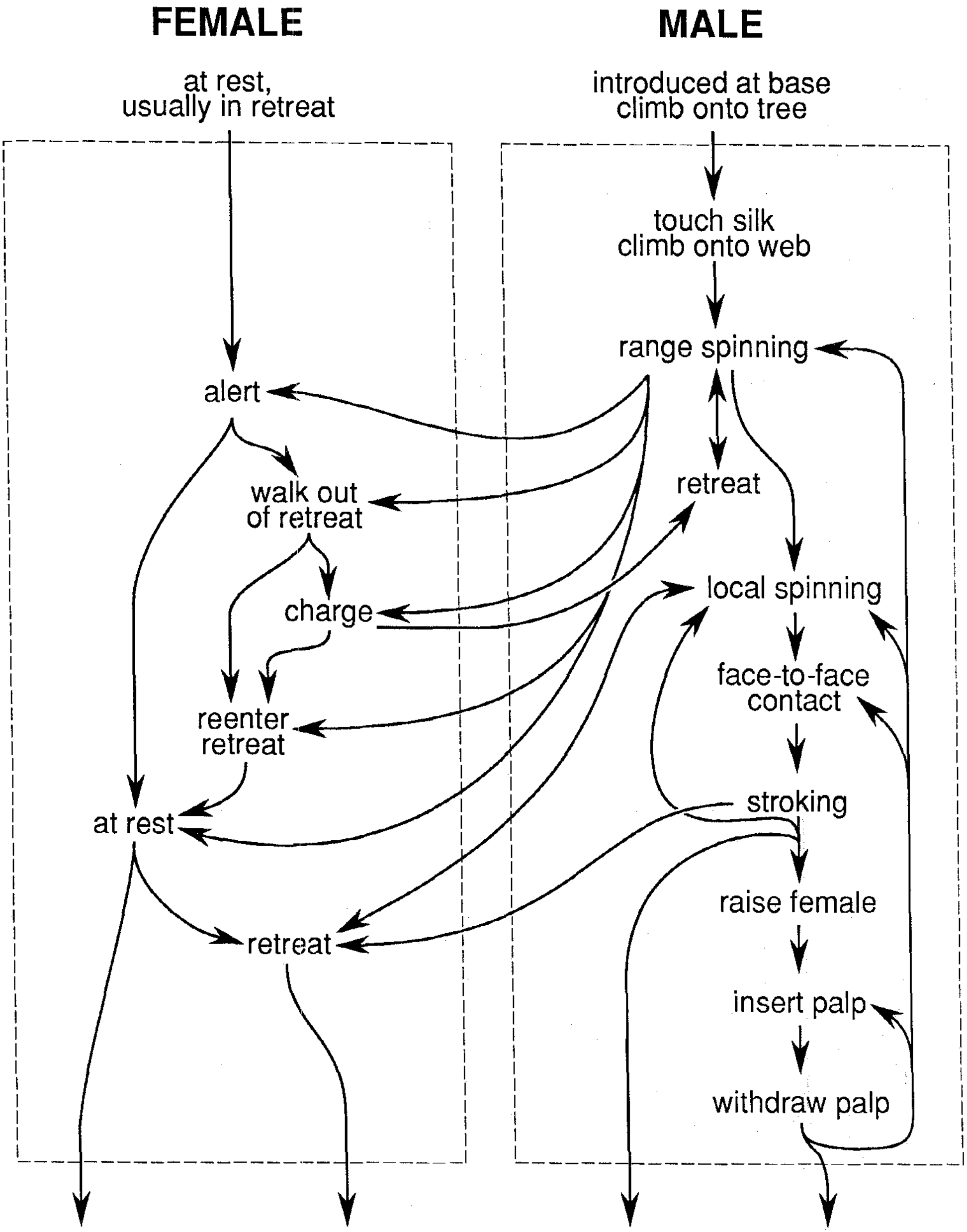

Fig. 5.—Diagram of observed sexual behavioral sequences of *D. volucripes*. Dashed lines delimit sexual behavior.

The sequences of female and male behaviors in *D. volucripes* are shown in Fig. 5. Jackson (1979) divided courtship in dictynids into a non-contact and a contact phase. This division is evident in *D. volucripes*, though I prefer to distinguish three phases. Ranging-spinning is purely a non-contact phase, local-spinning is a transition phase, and the stroking phase is purely a contact phase.

Sperm induction evidently takes place before the start of courtship, as it was not observed in any trial. It appears usual for dictynids to re-induce sperm soon after mating (Gerhardt and Kaestner 1937; Billaudelle 1957; Bristowe 1971), but we did not see this in *D. volucripes*.

The present results are consistent with Jackson's (1979) conclusion that vision has little or no role in dictynid courtship. The finding that males on recently vacated webs courted normally in the ranging-spinning and first part of the local-spinning phases likewise corroborates his conclusion that it is the female's silk which releases and directs courtship in his "non-contact phase".

Any study of courtship in spiders suffers from the burden that its principal function is not yet established. Despite decades of controversy (for a summary review see Robinson and Robinson 1980), the two main contending hypotheses remain the same: Successful courtship (a) inhibits a very predatory animal (the female) from attacking a very edible one (the male), or (b) stimulates the female to accept the male as a mate. The two hypotheses need not be mutually exclusive, but the question remains of which is the limiting factor in courtship evolution.

The predation-inhibition hypothesis is so attractive that it long had near hegemony among araneologists. For a recent explicit example of this view, see Gertsch (1979). T. H. Savory's repeated protest (e.g., Savory 1928) that sexual approach is in fact rarely hazardous for male spiders seems to have had little impact, possibly because other aspects of his view of courtship are so hard to accept. Recent studies (e.g., Jackson 1979; Robinson and Robinson 1980), however, increasingly support the view that courtship is mainly a matter of female mate-choice. That is to say, it requires little effort to inhibit the female's predatory drive, but much to gain acceptance as a mate. On a larger scale, this is in line with the view of animal courtship as shaped mainly by female choice and not by a need for species-recognition (Thornhill and Alcock 1983; West-Eberhard 1984; Eberhard 1985).

The present study was not made with either hypothesis in mind, but I believe it contributes to this question. I interpret the results as much more consistent with female choice than with a need to inhibit predation. Let me mention in passing that I reach this conclusion reluctantly, as the predation-inhibition hypothesis has always for me invested spider and scorpion courtship with special fascination. In none of the 13 trials was there any indication that the male was in serious danger. Only in a minority of trials did the female rush at or otherwise vigorously approach him, and in each case he easily retreated out of reach.

On the other hand, there were good indications of female choice. In three of 13 trials, normal courtship failed to lead even to a first insertion. In two of eight trials in which the male courted beyond the first insertion, he did not achieve a second insertion. There are further indications of mate-choice in the behavior of females. Females showed much less behavioral variety than males (Fig. 5) and after the initial reaction during ranging-spinning they mostly remained passive in the retreat. In a few cases the female retreated slightly from the male during local-spinning or stroking, apparently in resistance to courtship.

Mate-choice is also implied in raising the female prior to insertion. In the Results and Fig. 5, I treat this as an active process on the male's part and passive on the female's part. Although I cannot be certain of this, it had that appearance, and the first two pairs of legs are surely strong enough to raise another spider's body. At the same time, it seems clear that a female which grasps the substrate silk with flexed legs could not be lifted by force, and females sometimes appeared to resist in this way. In some trials the male was seen to repeatedly reach his legs

Table 1.—Period of hematodocha pulsation in dictynid spiders. Explanation in text. Billaudelle (1957) in fact specified 2-3 pulsations/s in *D. civica*, but I assume he meant one per 2-3 s.

SPECIES	PERIOD (seconds)	REFERENCE
Dictyna benigna	about 4-30 (increasing during time of insertion)	Karpinski 1882
Dictyna civica	2-3	Billaudelle 1957
Dictyna sublata	about 6	Montgomery 1903
Dictyna volucripes	2-10 (mostly 7-9)	this paper
Heterodictyna viridissima	about 10	Berland 1916

under the female's carapace in apparent unsuccessful attempts to raise her. The best interpretation of stroking, then, is that it serves to overcome resistance to raising.

The tendency to revert to courtship between insertions is part of the usual pattern in dictynids (Jackson 1979). The general lack of female aggression and her almost complete passivity at this time make it hard to reconcile such renewed courtship with any need to inhibit predation.

Jackson (1979) has reviewed the durations of insertions reported from dictynids. These are almost all between 15 min and 2 h, much like those recorded from *D. volucripes*. Pulsations of the hematodocha during mating have previously been timed in four species (Table 1). These mostly have a period of 2-10 sec, likewise in the range recorded in *D. volucripes*.

Prolonged cohabitation has been reported from several families of spiders, but seems especially prevalent in the Dictynidae (Bristowe 1971; Gertsch 1979; Jackson 1979). Together with the generally nonaggressive nature of sexual activity, this led Bristowe (1971) to remark on "the unusual friendship which seems to exist between the males and females" in this family. The adaptive basis for such cohabitation is unknown. At present the best hypothesis seems to be that it functions primarily in mate-guarding by males Jackson (1977).

If the function of cohabitation is obscure, its main social-evolutionary implication seems clear. Any mechanism which facilitates mutual tolerance among conspecifics removes a key obstacle to sociality. Cohabitation cannot explain why some dictynids are social, but it shows why they need not be solitary.

ACKNOWLEDGMENTS

In my first paper on arachnids I deem it suitable to acknowledge my teachers in the subject, C. D. Dondale and J. H. Redner of Canada Agriculture and R. E. Beer of the University of Kansas. This study began as a project in Dr. Beer's Arachnology class and has subsequently benefitted from advice and criticism by C. D. Dondale, W. J. Gertsch, R. R. Jackson and M. H. Robinson. S. Pierce assisted in collecting data. I also thank L. Moortgat for statistical advice, M. M. Starr for volunteer typing and G. Venable for preparing Fig. 5.

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