

Male Mating Strategies of Dictynid Spiders with Differing Types of Social Organization

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SYNOPSIS

The social organization of *Mallos trivittatus* and *Dictyna calcarata* is communal and territorial. These spiders live in web complexes which are divided into defended territories. *M. gregalis* lives in a communal and non-territorial social organization, in which hundreds of spiders share communal webs without territories. In the territorial species, the web itself releases courtship, and males discriminate between webs of conspecific females and those of other species and between webs of conspecific females and conspecific males. This response pattern is probably related to the relative rarity of encounters between males and females. In the non-territorial species, encounters between males and females are comparatively common, and female silk does not release courtship. Instead, the males seem to incorporate a sexual advertising routine into their activity budgets.

INTRODUCTION

Most web-building spiders, including most of the Dictynidae, tend to be solitary. Except for male/female pairs or females with their newly hatched progeny, one usually finds a single individual in each web, and webs are not connected to other webs by silk. However, there are some exceptional species, generally referred to as "social spiders" (for reviews, see Burgess, 1976; Krafft, 1970; Kullmann, 1968, 1972; Shear, 1970), in which large groups of individuals share a common web. One of these species is the dictynid *M. gregalis* (Simon) (Diguët, 1915; Burgess, 1976), which lives under a communal and non-territorial social organization (Jackson, 1977). In this species, hundreds of individuals of all sex and age classes tend to share a communal web on which they routinely feed in groups on the same prey items. Aggressive and cannibalistic behavior normally does not occur. Some other dictynids live in web complexes, in which they maintain a communal and territorial social organization. Web complexes consist of individual web units, connected to each other by silk and defended by the occupants. In these species aggressive and cannibalistic behavior is relatively pronounced, and it is exceptional that individuals feed in groups.

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In this paper, correlations between male mating strategies and the social organization of the species will be discussed. Four related questions were investigated. Does the web itself release courtship from the male? Do males discriminate between the webs of conspecific females and those of other dictynids? Do males discriminate between the webs of conspecific females and those of conspecific males? Do the answers to these questions vary with the type of social organization adopted by the species?

Combining and modifying the definitions of Manning (1972) and Morris (1956), courtship is defined as heterosexual communicatory behavior that forms the normal preliminaries to mating. The courtship behavior of three species, *M. gregalis* (communal, non-territorial), *M. trivittatus* (Banks) (communal, territorial) and *Dictyna calcarata* Banks (communal, territorial), has been studied in the laboratory. In each species, there is a phase of courtship during which the spiders are not in physical contact with each other. The male plucks on the web with his forelegs in a species-specific manner. During the contact phase that follows, the male presses his face against the female in a species-specific manner, and there may be periods of stroking with his palps, biting or pushing. Species-specific patterns of abdomen twitching occurred during both phases of every courtship interaction that has been observed for each species. This behavior was a valuable indicator of sexual response in these spiders because it usually occurred exclusively during intraspecific interactions.

METHODS

Maintenance

The laboratory colony of *M. gregalis* originated from spiders collected by J. W. Burgess, near Guadalajara, Mexico. These were maintained on large communal webs in the laboratory and fed adult house flies (*Musca domestica*) approximately every five days. *M. trivittatus* were collected in the Chiracahua Mountains of Arizona, and *Dictyna calcarata* were collected near Lake Chapala in Mexico by the author. These two species were maintained one per cage in the laboratory; and each cage was provided with continual moisture, through a wet cotton roll connected to the cage. Continual access to adult *Drosophila melanogaster* was provided by means of a culture of flies in a glass vial connected by a plastic tube to the spider's cage. These cages were built from 9-cm-wide transparent plastic petri dishes according to a design described earlier (Jackson, 1974). The *M. gregalis* used in the experiments reported here were kept in cages of this type also. One adult spider was kept in each cage, along with three to five immature spiders. Lights in the laboratory came on at 0800 and went off at 2000. Temperature was maintained at $24^{\circ}\text{C} \pm 1^{\circ}\text{C}$.

Testing Procedure

A test consisted of dropping the male onto an empty web and recording his behavior for 15 min. Each male was tested twice, on one day with one type of web and on the next day with another type of web. The pair of webs were built by either two different species or by males and females of the same species. There were four time slots for testing males: 0800, 0830, 0900 and 0930. Each male was assigned to a time slot and tested at this time on both days. In each series of tests for a given set of two types of webs, 20 males of a given species were tested. One-half were tested with one type of web on the first day (group A), and the other half were tested with the other type of web on the first day (group B). Since only four males could be tested over a two-day period, ten days were necessary for each series. Decisions were made randomly, using a random numbers table (Rohlf & Sokal, 1969). These decisions included selecting the spiders to be used from among those available in the laboratory, assignment of males to groups and to time slots, and selecting the particular web of each type with which to test each male. The statistical tests that were used are described by Sokal & Rohlf (1969).

Since there were 30 min between time slots, and each test lasted only 15 min, there was a 15-min period between successive tests. This time was used to prepare for the next test. Ten to fifteen minutes before the start of each test, the spider whose web was to be used was removed, and the male that was to be tested was removed from his web. To remove a spider from its web, it was prodded with a camel's hair brush into a transfer tube. A transfer tube is a 2- to 3-cm-long strip of transparent plastic tubing, fitted with a cork at each end.

To begin a test, the lid was removed from the cage containing the web, and the transfer tube was held over the web. If the male did not drop onto the web when the corks were removed from the tube, he was gently forced out with the camel's hair brush.

The age and sexual experience of the males were not known in most cases, since most males were collected as adults in nature, in the case of *M. trivittatus* and *D. calcarata*, or in laboratory communal webs, in the case of *M. gregalis*. To obtain the webs used in the experiments, spiders were placed in clean cages, one per cage. After three days, *Drosophila* were provided, and the webs were used seven to nine days later. All webs from females were built by virgins, two to five weeks after they reached maturity. Each of these females underwent her final molt in a laboratory cage, and they were kept isolated from males. No webs were used in more than one test, and not more than one web of a given spider was used. Also, no males were tested with more than one sequence of two webs.

For each minute of the 15-min observation period, a record was made of whether or not the male walked. The total number of minutes during which walking was seen provided an index of locomotion, 15

TABLE I

Behavior of males when tested on empty webs of females of different species

		Species of male			
		<i>Mallos gregalis</i>	<i>Mallos trivittatus</i>	<i>Dictyna calcarata</i>	
				Experiment No. 1	Experiment No. 2
Conspecific web	Abdomen twitch*	0	7(7) (2·1 ± 1·46 min)	10(9)‡ (1·8 ± 1·87 min)	11(7) (1·5 ± 1·04 min)
	Pluck or spin*	0	2(2) (2 min, 1 min)	1(1) (2 min)	3(3) (5 min, 1 min, 1 min)
	Locomotion	4·4 ± 4·59 min	3·4 ± 3·69 min	7·9 ± 3·22 min	6·9 ± 4·14 min
Contraspecific web	Contraspecific species	<i>Mallos trivittatus</i>	<i>Mallos gregalis</i>	<i>Mallos trivittatus</i>	<i>Mallos gregalis</i>
	Abdomen twitch*	0	0	2(1) (1 min, 1 min)	4(0) (1·3 ± 0·50 min)
	Pluck or spin*	0	0	1(1) (2 min)	1(1) (1 min)
	Locomotion†	3·3 ± 3·83 min	2·7 ± 3·51 min	5·6 ± 2·50 min	4·7 ± 4·58 min

* Total number of males that performed the indicated behavior. In the first set of parentheses, number of males that performed the behavior only when tested on the indicated type of web. In the second set of parentheses, mean ± s.d. or actual values for durations.

† Mean ± s.d.

‡ McNemar test, $p < 0.05$.

|| McNemar test, $p < 0.025$.

being the maximum and zero being the minimum possible value. Standing in a single location while grooming or performing elements of courtship behavior occurred at times, but locomotion also occurred during the same minute of observation in each case. In addition, indices of the durations of abdomen twitching and localized spinning were obtained by the same procedure.

RESULTS

Abdomen twitching occurred during tests with *M. trivittatus* and *D. calcarata*, but not during those with *M. gregalis* (Tables I and II). Also, four *M. trivittatus* males plucked on webs, and six *D. calcarata* performed localized spinning, which is another element of behavior associated with courtship in this species. During localized spinning, the male makes frequent turns as he spins in a limited area in a manner that has a more energetic and excited appearance than other forms of spinning. Each male that plucked or performed localized spinning also performed abdomen twitching during the same test. When abdomen twitching, plucking or localized spinning occurred, their durations were generally brief (Tables I and II).

M. trivittatus and *D. calcarata* discriminate between the webs of conspecific and conspecific females (Table I) and those of females and males (Table II). In the case of *M. trivittatus*, only conspecific female webs released abdomen twitching. Some *D. calcarata* males, however, also performed abdomen twitching on webs of *M. trivittatus* females. For this reason, another 20 males were tested with conspecific webs and webs of

TABLE II

Behavior of males tested on empty webs of conspecific males and females

		Species of male		
		<i>Mallos gregalis</i>	<i>Mallos trivittatus</i>	<i>Dictyna calcarata</i>
Female web	Abdomen twitch*	0	8‡ (1.9 ± 1.46 min)	10‡ (1.6 ± 1.26 min)
	Pluck*	0	2 (1 min, 1 min)	0
	Locomotion†	2.5 ± 3.03 min	2.7 ± 3.09 min	4.7 ± 4.80 min
Male web	Abdomen twitch*	0	0	0
	Pluck*	0	0	0
	Locomotion†	2.0 ± 1.95 min	2.9 ± 5.12 min	2.7 ± 3.27 min

* Number of males that performed the indicated behavior. In parentheses, mean ± s.d. or actual values for durations.

† Mean ± s.d.

‡ McNemar test, $p < 0.025$.

M. gregalis. Again contraspecific webs released abdomen twitching in a few cases. However, abdomen twitching was more often released from conspecific webs in both sets of tests. Although incidences of plucking on the web and localized spinning were infrequent and significance was not shown (McNemar tests), it is consistent that these motor patterns were seen most often on webs of conspecific females, and they were performed by communal, territorial males only. There was no indication that activity differed according to the type of web on which the male was dropped (Wilcoxon tests).

To summarize, webs released courtship from males of two communal, territorial species, but not from the males of the communal, non-territorial species (Table III). Some preliminary observations carried out in a more casual manner suggest that a longer period of observation would not significantly alter these results. Males were observed for 60 to 90 min after being placed individually on empty webs built by conspecific females. None of six observed *M. gregalis* males initiated courtship. Of four observed *M. trivittatus* males, two performed abdomen twitching within the first 15 min, but soon ceased. No plucking was seen, and no abdomen twitching occurred after the first 15 min.

TABLE III

Summary of relationship between social organization and the manner in which males respond to empty webs

	Species		
	<i>Mallos gregalis</i>	<i>Mallos trivittatus</i>	<i>Dictyna calcarata</i>
Social organization	Communal and non-territorial	Communal and territorial	Communal and territorial
Web is a releaser of male courtship	No	Yes	Yes
Males discriminate species of spider that built web	No	Yes	Yes
Males discriminate sex of spider that built web	No	Yes	Yes

DISCUSSION

The manner in which dictynid males respond to empty webs seems to be related to the type of social organization adopted by the species. In a web

complex of *M. trivittatus* or *D. calcarata*, there are individual web units, each of which may or may not be occupied by a female. Also, spiders of these species are occasionally found in isolated webs, not within a complex. A hypothetical mating system will be proposed for these species. Males wander about, encountering different web units. Upon encountering silk that was recently spun by a female, the male is alerted to her possible presence, and he begins to court. If the female is present, she responds by walking or plucking, and the male continues to court. If she is not in the web, the male soon ceases to court, departs from the web unit, and continues his search. The number of females with which a male mates is probably a major determinant of his reproductive success. A limiting factor may be the number of females that a male encounters. From this perspective, each encounter with a female is a relatively important event for the male. Related to this, a specific stimulus (female silk) releases courtship in the communal, territorial species.

The situation is different in *M. gregalis*. Males and females are continually in relatively close proximity to each other in a communal web in which there are no individual subunits analogous to those of the communal, territorial species. Encounters with females and silk laid by females must be frequent events for a male of *M. gregalis*, and the fact that silk alone is not sufficient to release courtship in this species would seem to be related to this. Furthermore, courtship and mating in *M. trivittatus* and *D. calcarata* can be staged, in a certain sense; but only spontaneously occurring courtship and mating were observed in *M. gregalis*. When a male of *M. trivittatus* or *D. calcarata* was dropped onto webs containing a conspecific female and observed for a period ranging up to several hours, courtship was observed in most cases. However, when the same types of observation were carried out with *M. gregalis*, courtship was not seen.

The number of females encountered would not seem to be a limiting factor for the reproductive success of *M. gregalis* males. However, the number of encounters with receptive females may be important. In the hypothetical mating system proposed for *M. gregalis* the male has an advertising routine that is structured into his activity budget, instead of courtship being released by specific stimuli. For a certain amount of time, perhaps each day, he advertises himself as a male that is ready to mate. These signals are broadcast instead of being directed at particular females. Pluck-walking, a form of behavior that would seem to fit this description, is rather frequently seen occurring spontaneously in communal webs in the laboratory. The male walks slowly, alternately plucking in the web with first one foreleg and then the other. Males pluck-walk spontaneously when they are in webs not containing females; and when in webs containing females, males that are pluck-walking are not always in the immediate vicinity of another spider.

Probably pheromones are involved in releasing courtship from males of *M. trivittatus* and *D. calcarata* that contact webs of conspecific females,

but further investigation is needed. Although sex pheromones in spiders have not received nearly the attention given this phenomenon in insects (Shorey, 1976), there is evidence of airborne sex attractants in certain web-building species in the families Araneidae (Blanke, 1973, 1975) and Dipluridae (Hickman, 1964). Crane's (1949) studies with salticids implicated an airborne pheromone that lowers the male's threshold for courtship in these spiders that do not build webs. In a number of species of Lycosidae, another group of vagabond spiders, when the male crosses the path of a female, he responds with searching and/or courtship behavior (Bristowe & Locket, 1926; Dondale & Hegdekar, 1973; Engelhardt, 1964; Farley & Shear, 1973; Hegdekar & Dondale, 1969; Hollander, Dijkstra, Alleman & Vlijm, 1973; Kaston, 1936; Koomans, van der Ploeg & Dijkstra, 1974; Richter & van der Kraan, 1970). The female's dragline may or may not be necessary, and the species specificity of the response varies with the species involved.

Foelix (1970) has described hairs from the legs and palps of araneid spiders that resemble the chemosensitive hairs of insects, and we might expect hairs of this type to be receptors for pheromones.

In the case of *M. trivittatus* and *D. calcarata* we do not know yet whether webs of mated females release courtship, since only the webs of virgins were used. Although females of these species will mate with more than one male before oviposition, there is the possibility that females regulate the production of courtship-releasing pheromones associated with their silk, in accordance with factors determining their receptivity. In several cases when males were placed on webs containing conspecific females that had mated previously with other males, several hours passed during which the courtship did not occur, after which the male was removed. Although there are other potential explanations, one possibility is that these females had shut off production of courtship-releasing pheromones.

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