Revue Arachnologique, 2 (3), 1979 : 103-132.

Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae)

II. The relationship between courtship, mating, agression and cannibalism in species with differing types of social organization

R.R. JACKSON*

(North Carolina Mental Health Research,
P.O. Box 7532, Raleigh, North Carolina 27611)

Contents

---

* Manuscrit reçu le 10 mai 1978; *adresse actuelle de l'auteur*: Zoology Department, University of Canterbury, Christchurch 1, New Zealand.

Résumé

L'organisation sociale chez les *Dictyna* et les *Mallos* comprend des espèces solitaires, des espèces qui vivent en groupes et gardent des territoires (grégaires, territoriales), et une espèce vivant en groupe (*Mallos gregalis*) qui ne conserve pas de territoires (grégaire, non-territoriale). Dans toutes les espèces, les mâles semblent être plus nomades que les femelles; les femelles, plus sédentaires. Les femelles s'accouplent avec plusieurs mâles. Les dimorphismes sexuels des chélicères et des palpes pourraient être importants quant à leurs moyens de communiquer entre eux. Par contraste avec les autres espèces, le *M. gregalis* n'est pas agressif, il vit à proximité de ses voisins et n'est pas cannibale. La façon de faire la cour et l'accouplement varient selon les espèces et à l'intérieur même de ces dernières; cependant la façon de courtiser chez les espèces agressives et cannibales ne semble ni plus complexe ni plus circonspecte que celle des *M. gregalis*. Ces observations jettent un doûte sur l'hypothèse avancée précédemment que la principale fonction de faire la cour chez les araignées est de protéger les mâles contre les femelles cannibales.

Summary

Social organization within *Dictyna* and *Mallos* includes solitary species, species that live in groups and maintain territories (communal, territorial), and a group-living species (*Mallos gregalis*) that does not maintain territories (communal, non-territorial). In all species, males seem to be more nomadic; females, more sedentary. Females will mate with more than one male. Sexual dimorphisms of the chelicerae and pedipalps may be involved in communication. In contrast to other species, *M. gregalis* is non-aggressive, close-spacing, and non-cannibalistic. Courtship and mating behavior vary within and among species; however, the courtship of aggressive and cannibalistic species seems no more complex or cautious than that of *M. gregalis*. These observations bring into question the previously proposed hypothesis that a major function of courtship in spiders is to protect males from cannibalistic females.

Introduction

In spiders, cannibalism has repeatedly been given major importance, either explicitly or implicitly, in discussions concerning the function of courtship (e.g., BRISTOWE, 1958; BRISTOWE & LOCKET, 1926; GERHARDT & KAESTNER, 1937; KRAFFT, 1970; PLATNICK, 1971; SAVORY, 1928; TURNBULL, 1973; WITT, 1975). Spiders are predators of arthropods, and the males of most species are within the size range of the prey of females. Observations in nature and especially in the laboratory indicate that female spiders sometimes kill and feed on conspecific males. Often the courtship behavior of males has a "cautious" appearance, with periods of approaching and withdrawing; and the female may rush toward the male in a manner appearing rather "violent". Observations such these might seem to compel the conclusion that spider courtship behavior is largely the result of natural selection related to cannibalism. In other words, the function of courtship tends to be viewed as reducing the probability that the male will be treated as prey by the female. This will be called the "cannibalism reduction hypothesis" for the function of male courtship. Although the views of some authors tend to be complex, allowing for other functions in addition to cannibalism reduction, some variation of the cannibalism reduction hypothesis is a nearly ubiquitous element in discussions of spider courtship. Sometimes it is an explicitly proposed function; other times it is merely implied.

The popular myth that female spiders usually prey on the males either during courtship or after copulation has been disclaimed many times by arachnologists. Sometimes the same arachnologists emphasize cannibalism reduction in discussions of the function of courtship. Perhaps cannibalism is not so frequent in spiders because of the effectiveness of courtship in preventing its occurrence, but this hypothesis needs critical investigation.

Some observations on the behavior of dictynid spiders that are relevant to the cannibalism reduction hypothesis will be discussed here. These spiders are of special interest because different species live under differing types of social organization (JACKSON, 1978a), and the cannibalistic tendencies of the species vary with their social organization. The majority of dictynids are solitary, each individual generally living alone in an individual web that does not touch other occupied webs. These are found especially on stems and leaves of shrubs and herbaceous plants. *Mallos trivittatus* Banks, *Dictyna calcarata* Banks, and *D. albopilosa* Franganillo are communal and territorial, living in web complexes that consist of individual web units connected to each other by silk. Although several individuals often occupy a single web unit, generally two adults of the same sex or two immatures of comparable size do not share the same web unit. Each individual web and each web unit consists of a catching area and a nest in which the spiders tend to remain when not active or feeding. *Mallos gregalis* Simon is communal and non-territorial, with hundreds of individuals sharing the same large communal webs which are not divided into web units. Females of *M. trivittatus* tend to be 7^{mm} in body length; males 5^{mm}. The other species in this study tend to be smaller; females approximately 5^{mm}, males usually 1^{mm} shorter.

Species with differing types of social organization will be compared with respect to courtship, mating, aggression, and cannibalism. Courtship is defined as heterosexual communicatory behavior that forms the normal preliminaries to mating (JACKSON, 1977a); mating is used as synonym for copulation. WILSON's (1975) definition of communication will be used: "Action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either or both participants." Signals are behavioral and other characteristics of an organism used in communication (OTTE, 1974). Aggression is behavior of one individual that reduces the freedom or fitness of another individual (WILSON, 1975), with usage restricted to intraspecific interactions for the present discussion. Cannibalism is intraspecific predation (FOX, 1975). Whether cannibalism is motivationally distinct from other forms of aggression (see HUNTINGFORD, 1976; MOYER, 1968) has not been determined for these spiders.

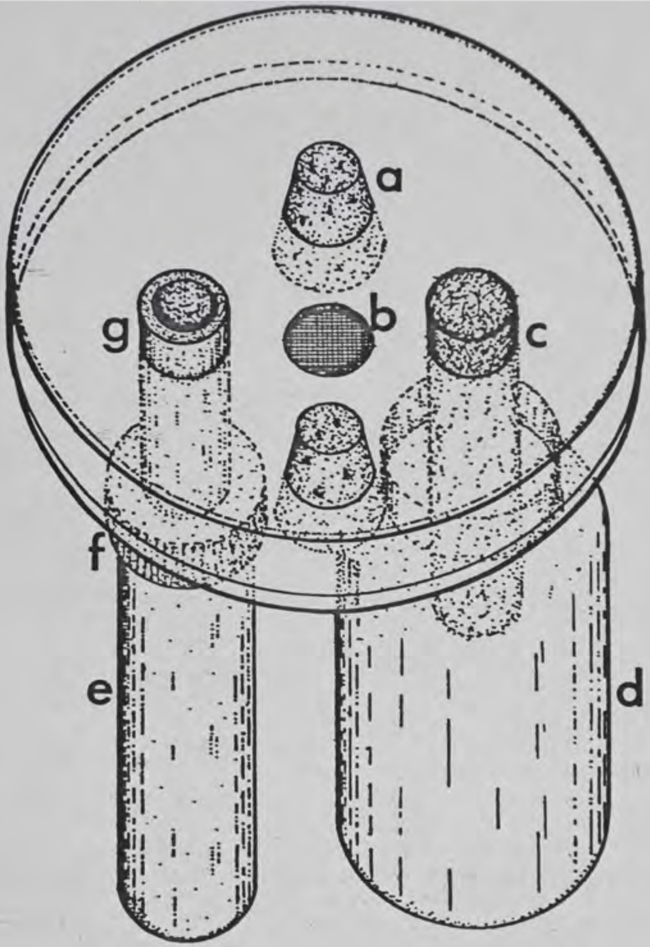


Fig. 1. – Maintenance cage constructed from clear plastic petri dish (diameter: 9 ^{cm}). Diameter of all holes: 1 ^{cm}. **a**: Hole plugged with cork. **b**: Hole covered by metal screen, for ventilation. **c**: Cotton roll (4^{cm} x 1^{cm}) inserted through hole. Opposite end set in glass jar (**d**) containing water, providing continual moisture to interior of cage. **e**: Culture of *Drosophila melanogaster* in glass vial. **f**: Plastic cap with hole. **g**: Plastic tube inserted at one end through hole in lid of culture vial and at other end through hole in cage. Flies emerge from culture and travel through tube into cage, providing continual food for spiders. Fresh culture vials substituted as necessary.

Methods and materials

General methodology will be described here. Specific methods used in studies of spacing and cannibalism will be given in the appropriate sections.

In the laboratory, *M. gregalis* in large communal webs were maintained on a diet of houseflies (*Musca domestica*), provided at approximately 5-day intervals. Temperature was maintained at approximately 24°C, and the light cycle was approximately 13 L: 11 D. There colonies were begun from spiders collected by Burgess (see BURGESS, 1976) in Guadalajara, Mexico. The webs in the laboratory were on plants and other objects, and they were not enclosed.

Small groups and single individuals of *M. gregalis* and single individuals of *M. trivittatus, M. niveus* O.P. Cambridge, and *D. calcarata* were also maintained in cages (fig. 1) similar in design to ones that have been used for other types of spiders (JACKSON, 1974). Since the dictynids tended to fasten their webs primarily to the corks and lower portion of the cage, the lid could usually be removed without substantially damaging the web. The usual diet was *Drosophila*, although occasionally adult *Musca domestica* (houseflies) were inserted through the cork holes as either supplementary or substitute prey. *M. trivittatus* and *M. niveus* were collected in Arizona and *D. calcarata* was collected in Jalisco, Mexico.

To observe interactions, one spider was introduced into the cage of another on the side most distant from the resident spider. A clear plastic tube (1^{cm} in diameter, 3^{cm} long) was used for transferral. The spider was pushed into the tube with a camel's hair brush, and the two ends were stoppered with corks. Then the lid was removed from the cage of the other spider, and the corks were removed from the tube. Holding the tube over the web, a brush was inserted through one end, forcing the spider from the other end and onto the web.

Whenever it was necessary to select spiders and assign them to groups, this was done with a random numbers table (ROHLF and SOKAL, 1969). The statistical tests used are described by SOKAL and ROHLF (1969).

Results

I. Elements of behavior

The following elements of behavior were discerned from observing *M. gregalis, M. trivittatus*, and *D. calcarata* in the laboratory.

1. Twich abdomen.

Abdomen twitching occurred intermittently in all three species during courtship, copulation, and intersexual interactions. It occurred both concurrent with other activities and while the spiders were otherwise inactive, and the details of this behavior differed among the species.

Similar behavior has been observed in numerous spider species (GERHARDT & KAESTNER, 1937), but its function is not clear in most cases. In a few species, this behavior is associated with stridulation (GWINNER-HANKE, 1970; LEGENDRE, 1963) or sound production when the abdomen strikes the substrate (HARRISON, 1969), but there is no evidence of either in the species considered here.

Abdomen twitching by males always occurred during courtship and sometimes occurred during male-male interactions. Occasionally females of *M. trivittatus* and *D. calcarata* twitched their abdomens when interacting with males. In *M. gregalis*, abdomen twitching tends to be relatively inconspicuous. The male's abdomen moves at a high frequency (estimated: 10 cycles per sec.) and low amplitude in the sagittal plane ("up and down"). In *M. trivittatus* and *D. calcarata*, the amplitude is greater and the frequency seems slower (estimated: 2 or 3 per sec.). In *D. calcarata*, movement is in the sagittal plane, as in *M. gregalis*. In *M. trivittatus*, movement is in the frontal plane ("back and forth").

2. Charge.

Charging spiders ran toward other spiders, over a distance of 1 to 2 ^{cm}, suddenly stopping before contacting the other spider.

3. Chase.

During chasing, one spider followed another with both moving rapidly. The chasing spider sometimes touched the chased spider with its forelegs. The duration of individual chases was usually approximately 1 sec. Females sometimes chased and charged towards courting males, and these elements of behavior frequently occurred during male-male and female-female interactions also.

4. Pluck and tap silk.

A number of different motor patterns can be described as plucking and tapping on the web. Although these movements were made primarily while the spiders were not in physical contact, occasionally they occurred briefly while the spiders were touching. Females, males, and immatures of each species tapped the web with their legs I during normal locomotion, even when not in the presence of other individuals. This tapping has a relatively smooth, slow appearance, as the spider waved its legs around, tapping the web several times with one leg then the other. During interactions between spiders, males and females of all species sometimes performed movements with some similarities to this tapping pattern, but with a more jerky, sudden, and rapid time-course and appearance (fig. 2). Both tapping (tarsi strike silk as legs move ventrally) and plucking (claws hold then release silk as the legs move dorsally) were seen at least occasionally when the interacting spiders were observed under a microscope. Behavior of this type was more common in courtship interactions, but also occurred during male-male and female-female interactions.

5. Jerk.

While standing in one location, *M. trivittatus* males sometimes suddenly and rapidly flexed all of their legs. Flexion of leg I was the most conspicuous. Only one jerk occurred at a time, followed by a pause of at least 1 sec. Occasionally males slowly walked forward as they intermittently jerked.

6. Quiver.

Superimposed on jerking, *M. trivittatus* sometimes undertook a series of very rapid, low amplitude movements of the body. (Jerking and quivering were seen during courtship only.)

7. Rock.

During courtship, males of *D. calcarata* sometimes rhythmically moved their bodies in the sagittal plane ("up and down") in a relatively slow, smooth manner, by alternately extending and flexing their legs.

8. Pluck walk.

This very distinctive behavior was performed by only the males of *M. gregalis.* It seems to constitute not only a component of courtship but also serves as a broadcasted sexual advertisement signal (JACKSON, 1978b). As males walked slowly through the web, they plucked in a rather jerky and rapid manner, 1 to 7 times with one leg I and then with the other. Each series of plucks with a given leg usually takes place in less than 1 sec. and the switch-over to the other leg occurred rapidly. If another spider was near, the male would stop walking and pluck in this manner briefly while standing in one location. Each leg I was held outward at approximately 45° to the sagittal plane during plucking. While his claws hooked around the silk, the male moved his legs I posteriorly and medially to pluck.

9. Sprint.

M. trivittatus males sometimes approached females by alternately walking, pausing, and sprinting. Sprinting was always preceded by a pause. Then the male suddenly moved forward very rapidly over a distance of a few milimeters (sometimes taking only a single step).

10. Interplay of legs.

When the legs of two spiders interplayed, primarily the legs I were involved (fig. 3). The legs of the two spiders repeatedly touched and moved slowly. This behavior has not been recorded in detail, but no particular pattern or stereotype was evident. Interplay of legs was seen during every type of interaction of each species. In *M. gregalis* this was virtually the only type of behavior that was seen when females or immatures encountered each other, and even this did not seem to occur in most cases, with the spiders simply changing directions and walking away.

11. Stroke and tap with legs.

During courtship, females and especially males of all three species may stroke and tap, with their legs I and sometimes with their legs II, on the legs, cephalothorax, and especially abdomen of the other spider. The form of these movements has not been recorded in detail.

12. Touch with face.

A distinctive and frequent element in the courtship of all species observed was for the male to bring his face (i.e., anterior cephalothorax) into contact with some part of the female's body (fig. 4). Every copulation observed was preceded by episodes in which the male and female touched face-to-face. Touching face-to-face occurred also during male-male interactions of each species.

Various aspects of touching with faces differed among the species. While touching females with their faces, male *M. gregalis* generally made stroking movements with their

Fig. 2. – *Mallos trivittatus* male taps silk with legs I just before touching female (on right, facing away from male, abdomen only in view).

Fig. 3. – *Mallos trivittatus* male (left) and female (right). Interplay of legs.

Fig. 4. – *Mallos trivittatus* male (left) and female (right). Touch with faces. Male's palps extend forward and stroke female. Male's chelicerae open, in preparation to bite female's chelicerae.

Fig. 5. – *Mallos trivittatus* male (right) begins to move under female (left) just before copulation. Female elevates cephalothorax. Sagittal planes of the two spiders are angled 45° to 90° to each other.

palps touching the females. Virtually any part of the female's cephalothorax and abdomen might be touched, although the most common location was the female's face and, just before or after copulation, her ventral abdomen.

Males of *M. trivittatus* moved their palps during touching also, but in this species the movements were of greater amplitude than in *M. gregalis*. When touching the female's face, the male tended to wedge his moving palps between those of the female, stroking her chelicerae with the dorsal surface of his palpal tarsi. The palps were sometimes extended forward somewhat (fig. 4). Males sometimes extended their palps as they approached females before touching. During the approach the male's palps sometimes rotated. (Each palp rotated in the opposite direction from the other.) When touching each other's faces, both spiders tended to have their fangs partially opened (i.e., lowered from the basal segments of the chelicerae). Males were seen with their faces touching the faces and the ventral bodies of females, and the latter occurred just before copulation only.

When *D. calcarata* males touched females with their faces, their palps were held at the side of the cephalothorax. The fangs were held open somewhat. Almost any part of the female's abdomen or cephalothorax might be touched, but by far the most common was for the male to touch the female's chelicerae with his own. Both spiders tended to have fangs open somewhat. The male's chelicerae were extended forward by tilting his cephalothorax dorsally and posteriorly with respect to the abdomen. Sometimes the male simply touched the female briefly with his chelicerae then backed away before repeating. Other times, he stroked her face with palp movements of relatively small amplitude and slow frequency, as in *M. gregalis*. The distal ends of the male's chelicerae touched the anterior surface of the female's. Sometimes the male also placed his anterior cheliceral surface under the distal ends of the female's chelicerae, such that the female's fangs rested on his chelicerae. From this position the male moved his palps up and down, stroking the female's chelicerae.

13. Bite.

The fangs of *M. trivittatus* (fig. 4) and *D. calcarata* males sometimes moved somewhat while they were held against the female's chelicerae. More conspicuous forms of biting, associated with lunging, will be described for *D. calcarata* females and *M. trivittatus* males. Often during touching with face, a male *D. calcarata* would position his chelicerae around a palp or chelicera of a female, and the chelicerae of the male sometimes closed against the female's for approximately 1 sec.

14. Lunge.

Sometimes males of *M. trivittatus* stationed themselves immediately in front of facing females and intermittently lunged forward with their chelicerae open and palps spread apart, touching the female's face momentarily at the most forward part of the lunge. Between each successive lunge, the male paused for a sec. or longer. At first the male might not be sufficiently close for lunges to bring his face into contact with the female's. Later his face might be continually in contact with the female's, with the forward part of the lunge serving to briefly push against the female's face.

Females of *D. calcarata* sometimes lunged, with chelicerae open, toward facing males. On the forward part of the lunge, a palp or chelicera of the male sometimes was positioned between the female's chelicerae; and the female sometimes closed her chelicerae against the male for approximately 1 sec. or less before backing away. This also happened once in *M. trivittatus*, but the other way around, with the male lunging at the female and briefly biting a palp or chelicera.

15. Push.

During pushing, two spiders touched face-to-face; and one or both walked or attempted to walk forward, causing the other spider to move backwards. Usually it was the female that pushed the male backwards during courtship. Pushing was seen during male-male and female-female interactions in each species, also.

16. Ram.

During male-male interactions *D. calcarata* were once seen repeatedly running towards each other, over a distance of a few mm and bringing their open chelicerae into contact briefly before backing away. This behavior had a rather violent appearance.

II. Organization of behavior during interactions in the laboratory

Courtship behavior can be divided into two phases depending on whether the two spiders were in physical contact with each other. Interactions normally began with non-contact behavior, such as the male plucking on the web and the female charging or lunging toward the male. The contact behavior that followed included stroking with the palps and legs, biting, interplay of legs, and similar behavior. Copulation sometimes followed contact behavior, or there could be repeated episodes of non-contact behavior. Also, episodes of copulation might be interspersed with periods of additional contact or non-contact courtship; and there were sometimes periods of courtship after copulation, not followed by further copulation. Frequently the females were inside or near their nests during courtship and copulation. During courtship, either the male, female, or both sometimes entered and departed the nest a number of times.

As in most spiders, vision seems to be of little or no significance during courtship in dictynids. A reasonable hypothesis is that communication is primarily by means of vibratory signals transmitted through the silk during non-contact behavior and by tactile and chemotactic signals during contact behavior. The possibility of olfactory communication should be considered also.

Male-male and female-female interactions had considerable similarity to courtship. Both contact and non-contact behavior occurred, frequently in alternation. Non-contact behavior included, among other things, plucking on the web and charging toward the other spider. All three types of interactions shared some elements of behavior, but a greater repertoire was generally present during courtship. During all types of intraspecific interactions, there were frequently interspersed periods during which one or both participants were inactive or walking about in the web. Sometimes walking was associated with frequent pauses and changes of direction, taking an appearance somewhat different from locomotion that occurred in the absence of a conspecific individual. Durations of all types of interactions tended to be variable (table 1). However, all intrasexual interactions lasted less than 20 min., suggesting that these tend to be shorter than courtship, but more extensive observation is needed.

Species	Type of interaction	Observation	Duration	End
Mallos trivittatus	Male-female	1	1 min	mate
		2	3 min	mate
		3	4 min	mate
		4	10 min	mate
		5	12 min	mate
		6	13 min	mate
		7	5 min	interrupt
		8	8 min	interrupt
		9	19 min	interrupt
		10	20 min	interrupt
		11	4 min	desist
		12	11 min	desist
	Male-male	1	1 min	desist
		2	1 min	desist
		3	9 min	
	Female-female	1	2 min	desist
		2	14 min	desist
		3	18 min	desist
Dictyna calcarata	Male-female	1	3 hr 51 min	mate
		2	8 hr 10 min	mate
		3	27 min	cannibalism
		4	5 min	desist
		5	7 min	desist
		6	10 min	desist
		7	12 min	desist
		8	20 min	desist
		9	2 hr 51 min	desist
	Male-male	1	5 min	desist
		2	8 min	desist
		3	15 min	desist
	Female-female	1	3 min	desist
		2	6 min	desist
		3	11 min	desist

Table 1. – Duration of interactions. Recorded until beginning of copulation, until cannibalism occurred, or until the 2 spiders stationed themselves at opposite ends of the cage and did not interact further for at least 20 min (desist). Interrupt: when the pair adopted the copulatory position, they were manually separated with a brush before copulation actually began.

III. Mating in the laboratory

1. Posture.

In each case, immediately before copulation the spiders were face-to-face and touching. Next the female's body became elevated and the male moved underneath her cephalothorax and engaged his palpal organ (fig. 5). The postures adopted by the species observed in this study and those described by other workers for other dictynids (see table 2 for reference) correspond to GERHARDT and KAESTNER's (1937) position I, in which the male moves under the female from her anterior end and his dorsal body surface may parallel the female's ventral, or he may make an angle with her body. In the dictynids in this study, the angle varied within a range from 45° to 90° for a single species and even during a single copulation. This was surprising since GERHARDT and KAESTNER noted that the copulatory angle adopted by a given species tends to be constant.

Species	Observation	Duration
Mallos gregalis	1 2 3	100 min.[a] 21 min.[b] 11 min.[b]
Mallos trivittatus	1 2 3 4 5 6	8 hr.[c] 60 min. 47 min. 39 min. 28 min. 22 min.
Dictyna calcarata	1 2	78 min. 43 min.
Dictyna civica	BILLAUDELLE (1957)	14 min.
Dictyna latens	LOCKET (1926)	15 min.
Dictyna uncinata	GERHARDT (1924)	30 to 60 min.
Dictyna volupis	MONTGOMERY (1903)	1 to 2 hr.
Ixeuticus longinuus	GREGG (1961)	1 to 2 hr.

[a] Performing non-contact courtship when first observed. Possibly copulation had preceded observation period.

[b] Copulation in progress when observation began.

[c] Estimated.

Table 2. – Copulation durations in laboratory, recorded as time during which male palps were applied to female epigynium (intervals of other behavior between periods of palp application deleted). Numbered observations were from the present study.

Also, the males of these species rotated their bodies during copulation such that the sagittal plane of the male and that of the female made an angle with each other ranging from 0° to 90° (fig. 5). I am not aware of previous reports of this sort of rotation during copulation in spiders. The male's legs I and II tended to be touching the female's body during copulation, and their exact positions were variable, but in general they wrapped around the female's cephalothorax and abdomen. Frequently there were periods during which the male rhythmically pulled on the female's body with these legs while the palpal hematodocha pulsated.

2. Duration.

Durations of copulations seen in this study, plus those reported in other studies, are given in table 2. Since there tends to be considerable intraspecific variability, more extensive data are needed in order to clarify how durations vary interspecifically. The longest copulation (8 hr; *M. trivittatus*) was an estimate, since I was away from the laboratory inadvertently on three occasions during this time (45 min, 35 min, 15 min). During the time of observation, there were interspersed short periods of courtship and inactivity, especially in the late afternoon, totaling approximately 30 min. BILLAUDELLE (1957) reported observing more than 50 copulations of *Dictyna civica*, each of which lasted 14 min. This remarkable consistency contrasts with the great variability observed for the species in this study.

3. Pattern of palp application.

The dictynids apply one palp at a time. The pattern in which the two palps are used seems to be variable. For example, in the case of observation n° 1 for *D. calcarata* (table 2), one palp was applied for 75 min, then the male walked away from the inactive female, and resumed courtship, with frequent periods of inactivity. Almost 1 hr later, the other palp was engaged for 3 min. After this the female became active, and the pair separated for the final time. During observation n° 1 for *M. gregalis* there were interspersed episodes of contact courtship between palp engagements, and the same palp was engaged twice in succession before switching to the opposite side. A single palp engagement occurred during the other two observations for *M. gregalis*. With one exception, during each copulation involving *M. trivittatus* and *D. calcarata*, each palp was applied only once, and there were periods of courtship between each palp application. The exception was the 8 hr copulation of a pair of *M. trivittatus* that was not observed in its entirety. Three applications of the left and four of the right palp were observed, and once the right palp was applied twice in succession.

4. Receptivity.

Males of each species studied in the laboratory readily mated with more than one female. Sometimes previously mated females of both *D. calcarata* and *M. trivittatus* remated with a different male on another day, after having become gravid with eggs. In one instance, I separated a pair of *M. trivittatus* (female had mated previously with another male) with a brush just as they began to copulate. The female subsequently oviposited fertile eggs, demonstrating that females of this species will mate with a second male even while carrying fertile sperm from a previous copulation. Females of *D. calcarata* and *M. trivittatus* will also mate after oviposition. Information is not presently available concerning *M. gregalis* females; and the relation between insemination, oviposition, and receptivity is generally poorly understood for spiders.

IV. Observations from the natural habitats of the spiders

Because observations of intraspecific interactions in the field are comparatively rare for spiders, those recorded in this study are reported individually in table 3.

It has been proposed that males of communal, territorial species are more nomadic and females are more sedentary, with males walking about within the web complex or the general environment rearching for females (JACKSON, 1978b). The same hypothesis would seem to apply to solitary species. Some observations relevant to this hypothesis will be mentioned here. In a large web complex of *M. trivittatus* in Arizona, estimated to contain 10,400 spiders, 11 males, compared to 6 females and 4 immatures, were seen walking. The estimated ratios of each sex/size class in the web complex were 9.3% males, 26.7% females, and 64.0% immatures (JACKSON and SMITH, 1978). On two separate occasions, males of the solitary species *D. tridentata* Bishop and Rudeman were seen walking on an outdoor table, not in the immediate vicinity of webs. Another six males were found inside webs. In contrast, all 25 females and immatures of this species that were found were located inside webs.

V. Spinning behavior during courtship

BRISTOWE (1958) reported that males of *Dictyna arundinacea* L. construct a special "chamber" or "mating canopy", presumably with similarities to the nest of the species in this study, inside which the pair copulate and later reside for a period of a month or more. The spinning behavior of *D. tridentata* males (table 3) suggests the possibility of something similar in this species. Also, once a male *M. gregalis* was seen spinning at a nest, with a female standing approximately 1 $^{\text{cm}}$ away; and once a male *M. trivittatus* spun briefly during courtship in the laboratory. In each case, the male spun rapidly, with frequent changes in direction, and sperm webs were not constructed. Since spinning is an integral part of courtship in some species of Thomisidae, Salticidae, Araneidae, and other groups of spiders (BRISTOWE, 1958; GRISWOLD, 1977; JACKSON, 1977b), the possibility that spinning in dictynids has a communicatory function should be investigated.

VI. The role of sexual dimorphism in communication

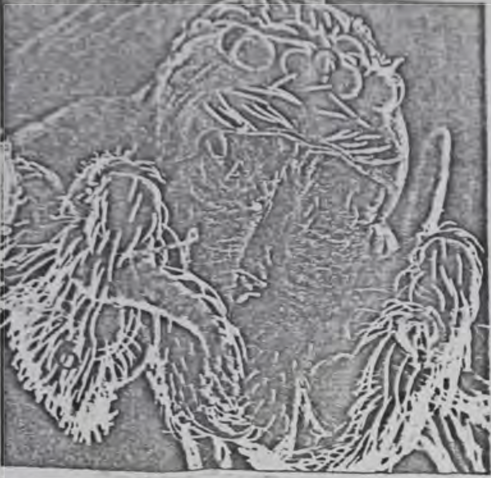
Pronounced sexual dimorphism tends to occur in the shape and size of chelicerae of adults in the genus *Dictyna* (CHAMBERLIN and GERTSCH, 1958), those of males being larger and more curved (compare fig. 6 and 7). Females of *Dictyna walckenaeri* Roewer use their chelicerae to grip those of the males (BERLAND, 1916; quoted vice versa by BRISTOWE, 1958). The chelicerae of *D. calcarata* are bow-shaped, and those of males are larger and more curved than those of females (fig. 6 and 7). In contrast, the chelicerae of *M. gregalis* and *M. trivittatus* are not bow-shaped (fig. 8). Males of *M. trivittatus* and both males and females of *D. calcarata* sometimes placed their chelicerae around a palp or chelicera of another spider during courtship. None were seen to place their chelicerae around both chelicerae of their partners simultaneously, as in *D. walckenaeri.* Further studies should consider the possibility that differences in cheliceral shape

Species	Type of interaction	Observation	Elements of behavior	Description
Mallos trivittatus	Male-female	1	Twitch abdomen (M), pluck and and tap silk (M), interplay of legs (M & F), charge (F), chase (F).	M repeatedly returned and courted after F chased.
	Male-female	2	Same as 1	Same as 1
	Male-female	3	Same as 1	Same as 1
	Male-immature	4	Twitch abdomen (M), pluck and tap silk (M), interplay of legs (M & I), chase (I).[1]	I (6^{mm}), initially inside nest, departed nest to chase M.
	Male-male	5	Twitch abdomen (n.2), pluck and tap silk (n.2), interplay of legs (n.1 & n.2), chase (n.1)[1]	M n.1 inside nest initially; M n.2 outside. n.1 departed nest to chase n.2.
	Immature-immature	6	Chase (n.1)[1]	I n.1 (4^{mm}), I n.2 (3^{mm})
	Female-female	7	Interplay of legs (n.1 & n.2), chase (n.1)[1]	Both on "extension line" (JACKSON, 1978a), F n.1 closer to nest.
	Female-female	8	Interplay of legs (n.1 & n.2), chase (n.1)[1]	Large diptera (Tipulidae) lands on web. n.1 departs nest and begins to feed. n2 arrives from neighboring web unit 10 sec later
	Female-immature	9	Chase (F)[1]	Large diptera lands on web. F departs nest and begins to feed. I arrives from interstitial area.

	Male-male	1	Twitch abdomen (n.1 & n.2), push (n.1 & n.2), chase (n.1)[1]	
Dictyna calcarata	Male on empty web unit	2	Twitch abdomen, pluck and tap silk	Enters nest, walks inside briefly, then departs web unit.
Mallos niveus	Male-female	1	copulate	Male-female angle: 90°
Dictyna tridentata	Male-female	1	Twitch abdomen (M), touch with face (M & F), push (F), chase (F)	M spins in and near nest. F feeds on Diptera, 8^{cm} away. F departs prey and goes to M. After chase, F returns to prey and M returns to spinning near nest.
	Male-female	2	Same as 1	Same as 1, except no prey presen present. F mostly inactive, a few cm from M.

[1] Chased individual departed web unit and did not return. Chasing individual either did not depart the web unit or departed and then returned.

Table 3. Interactions observed in nature. Elements of behavior described in text. Body lengths of immatures given in parenthesis. M: adult male, F: adult female, I: immatures.



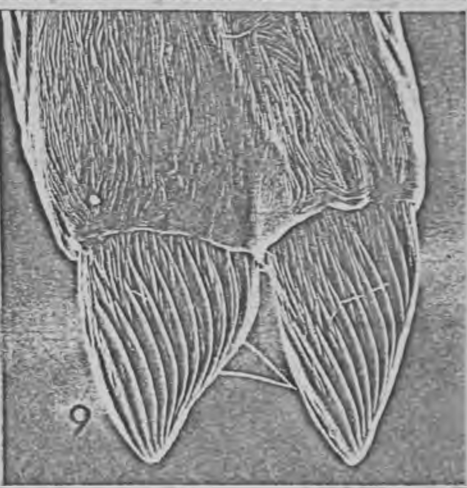


Fig. 6. – Face of *Dictyna calcarata* male (scanning electron micrograph). **c**: Bow-shaped chelicerae. **o**: Ocular region of cephalothorax. **h**: Hematodocha. **s**: Palpal spur (enlarged in fig. 9). Distance between inner of two chelicerae at widest point of bow: 100 u.

Fig. 7. – Face of *Dictyna calcarata* female (S.E.M.). **o**: Ocular region. **c**: Chelicerae (less bow-shaped than those of male, fig. 6). Same scale as fig. 6.

Fig. 8. – Face of *Mallos trivittatus* male (S.E.M.). **o**: Ocular region. **c**: Chelicerae (not bow-shaped, as on *Dictyna calcarata*, fig. 6 and 7). Distance between the inner edges of two antero-medial eyes: 100 u.

Fig. 9. – Tip of palpal spur of *Dictyna calcarata* male (S.E.M.). Diameter of spur at upper end of photograph: 50 u.

constitute signals during touching with faces and biting during the courtship of dictynids.

Another striking case of sexual dimorphism in *D. calcarata* is the spur on the palpal tibia of the males (fig. 7 and 9). Although it seems probable that this structure is involved as a signal, there is little evidence as to function at this point. Usually, when spiders touched faces, the male's palps were held at the side of the chelicerae in a position such that the spurs pointed dorsally and did not contact the other spider. However, when the male positioned his chelicerae under those of the female and stroked her with his palps, the spurs rubbed against the female's chelicerae. Also the spurs contacted the female's abdomen when the male touched the female with his face just before copulation. The relatively few observations made on this species should be emphasized; and we should be prepared for the possibility that the spurs are employed, on a relatively infrequent basis, in a more distinctive fashion. For example, in the salticid spider *Phidippus johnsoni* Peckham and Peckham, some of the more distinctive elements of courtship behavior occurred in only a small fraction of the observed interactions (JACKSON, 1977b).

VII. Aggression

1. General comments.

Since the behavior of males during male-female interactions was associated with mating or attempts to mate, this was referred to as "courtship." Interactions involving other combinations of spiders (male-male, etc.) led to one individual departing from the vicinity of the other, and the behavior involved will be referred to as "aggressive". This type of behavior occurred readily when male-male and female-female pairs of *M. trivittatus* and *D. calcarata* were placed together. In general, spiders of these species will not tolerate close proximity of other individuals of the same sex and size class (JACKSON, 1978a).

In contrast, aggressive behavior was extremely rare in *M. gregalis*. On two occasions I observed male-male pairs pushing and chasing (another observation, S.E. SMITH, personal communication), but usually males that encountered each other simply walked away. Behavior of females, such as charging and chasing males, seems to be related to unreceptivity and interference with mating attempts by the male. These motor patterns can be called "aggressive," and this type of aggressive behavior was seen in *M. gregalis*, as in the other two species. In general, individuals of all sex and age classes of *M. gregalis* lived in close proximity, frequently touching and walking over each other, without apparent aggressive behavior.

2. Aggressive behavior in the presence of prey.

In *M. gregalis*, groups of spiders routinely fed together on the same prey. Sometimes flies became completely covered by feeding spiders (fig. 10). Individuals that arrived after this point walked around on the feeding spiders, making no attempt to drive away other individuals to make room for themselves, and eventually simply walked away.

In *M. trivittatus*, sometimes more than one spider fed on the same prey item. However, unlike the situation of *M. gregalis*, this was the exception instead of the rule in *M. trivittatus*, occurring in only 5 of the 58 observed cases of feeding in the field. In each case the spiders were relatively widely spaced around the prey. 1. A female and male fed at opposite ends of a tipulid fly (3 $^{\text{cm}}$ apart). 2. A male and an immature (body length:

5^{mm}) fed at opposite ends of a Diptera (1^{cm}). 3. A male and two immatures (each 2^{mm}) fed on a tipulid. 4. A female fed with an immature (3^{mm}) on a tipulid. 5. Another female fed with an immature (3^{mm}) on a tipulid. In this case, prey capture was witnessed. The fly landed on the web and became stuck. The female rushed out and began to feed, followed soon by an immature from the same web unit. An aggressive interaction followed in which the female pushed and chased the immature; the immature returned repeatedly; and the female eventually tolerated the immature at the fly. Other aggressive interactions involving prey are summarized in table 3.

In each of 13 observations of feeding in nature by other species (*M. niveus*, *M. dugesi* Becker, *D. calcarata*, *D. tridentata*, *D. completa* Chamberlin and Gertsch, *D. phylax* Gertsch and Ivie), only one individual fed on a given prey (JACKSON, 1977c). However, it seems likely that feeding in small groups occurs occasionally in other communal territorial species, as it does in *M. trivittatus*, since joint feeding by a male-female pair of *D. calcarata* was seen in the laboratory. A male-female pair of *D. calcarata* was kept together, observed intermittently, and fed houseflies (*Musca domestica*) for 14 days after mating. Generally the spiders remained on opposite sides of the cage, although once they were observed feeding on the same fly. Feeding in pairs may also occur in some solitary species, in which males share webs with subadult and adult females (JACKSON, 1978c). Although not yet seen in the species in this study, BRISTOWE (1958) reported that male-female pairs of some European species will feed together on the same prey.

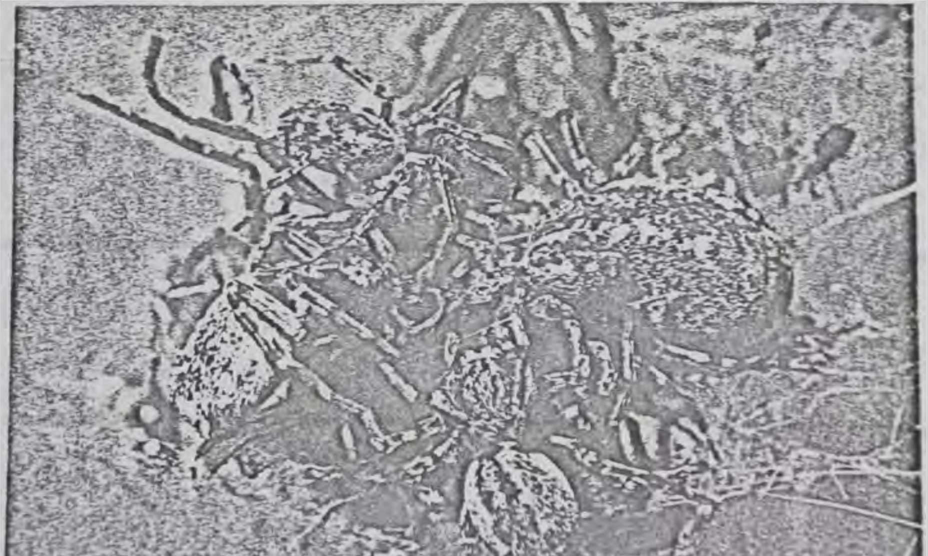


Fig. 10. – Group of *Mallos gregalis* feeding on the same fly. **f**: Adult female. **i**: Immature.

VIII. Spacing tendencies

1. Introduction and methods for recording spacing.

In *M. gregalis*, individuals of all sex and age classes were generally seen in close proximity of other individuals. In *M. trivittatus* and *D. calcarata* greater distances between individuals usually occurred. This difference is probably related to differences in aggressive behavior. In the laboratory, a systematic observation procedure was devised for recording the differing spacing tendencies of these species.

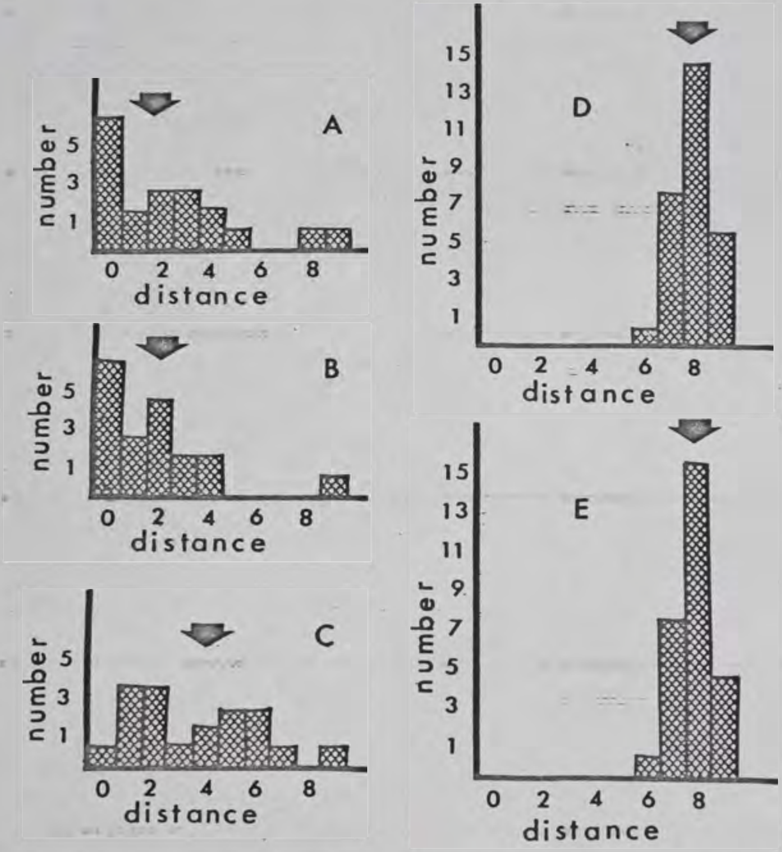


Fig. 11. – Interindividual distances of pairs of spiders in laboratory cages (cage diameter: 9^{cm}). Mean for 4 observations, recorded to nearest cm, was used for each pair. **0**: Members of pair in physical contact. **1**: Members of pair 1^{cm} or less apart, but not touching. 2: Members of pair between 1 and 2^{cm} apart. Etc. Arrows: means for all pairs. **A**: *Mallos gregalis*, adulte female, 20 pairs. **B**: *Mallos gregalis*, immatures, 20 pairs. **C**: *Mallos gregalis*, adult males, 20 pairs. D: *Mallos trivittatus*, pooled data for each sex/age class very similar. E: *Dictyna calcarata*, pooled data for 10 pairs each of adult females, immatures, and adult males. Data for each sex/age class were very similar.

Cages were of the same type used for maintenance (fig. 1), except that there was no cotton roll or *Drosophila* culture, and all four holes were plugged with corks. Two individuals of the same species and age/sex class were placed inside each cage at 1400 hr. On the following day, a record was made of the distance apart of the two spiders in each cage at 1100 hr, 1300 hr, 1500 hr, and 1700 hr. (Lights on, 800 hr; off 2000 hr).

2. Results and discussion.

During the day, spiders were relatively inactive. Only three were seen walking at the time of observation. Variation in the distance apart for a given pair through the day was small (mean within pair S.D.: 0.72^{cm}).

Pairs of *M. gregalis* spaced more closely together than *M. trivittatus* ($P<0.001$) and *D. calcarata* ($P<0.01$; Mann Whitney; pooled data for all sex/age classes)(fig. 11). This will be interpreted as a tendency of *M. trivittatus* and *D. calcarata* to maintain relatively large individual distances (HEDIGER, 1950) with respect to members of the same sex. *M. gregalis* females and immatures (pooled data) space more closely than males ($P<0.01$; Mann Whitney). Close spacing by females and immatures in these observations is probably related to a tendency of these spiders to aggregate and live in high densities on communal webs. The significance of wider spacing by males of *M. gregalis* may be related to sexual competition, since maintenance of an individual distance by a male might reduce interference by other males during courtship and mating. However, interference of this type has not been seen thus far in this species.

In nature, small immatures of *M. trivittatus* and *D. calcarata* were sometimes situated 1^{cm} or closer to larger immatures and adults. Adult male-female pairs sometimes shared web units. Males of *M. gregalis* might be expected to space more closely to females than to other males. Future studies should explore the spacing relations of heterosexual pairs and groups of immatures of varying sizes with and without adults.

IX. Cannibalism

1. Miscellaneous observations.

Observations in nature and the laboratory indicate that while other dictynid species tend to be cannibalistic, *M. gregalis* is almost never cannibalistic. In the communal webs in the laboratory, only two instances of cannibalism involving *M. gregalis* have been seen, despite a great many hours spent by several investigators observing these spiders. How the two cases of cannibalism came about is unknown. One case was a female feeding on a male, and the other was a female feeding on an immature. Once a small communal web in a $10\times10\times7^{cm}$ plastic cage, containing approximately 20 individuals of all sex/age classes, was kept without flies (water provided) for three weeks and watched casually. Although the spiders frequently touched and walked over each other, there was no evidence of cannibalism. P.N. WITT maintained a similar communal web without flies for 4 weeks without seeing cannibalism (personnal communication).

In contrast to *M. gregalis*, both direct and indirect evidence of cannibalism was relatively common for other dictynid species. 1. During a male-female interaction in the laboratory, a female *D. calcarata* killed and ate a male after 27 min of courtship.

Immediately beforehand the female had been pushing the male. Then she moved over the male and inserted her fangs into his carapace. The remaining observations were from the field. 2. Twice adult females of *M. trivittatus* were seen feeding on other adult females of approximately the same size. 3. Three dead females and two dead immatures were seen, each in a different web unit of *M. trivittatus*. In each case, an adult female occupied the web unit; the dead spiders had the appearance of eaten prey (dry; collapsed abdomens); and the dead spider was at the periphery of the web. The remaining cases involve solitary species. 4. A dead male was found in a web with a female of *Dictyna* sp. (Querecho Plains, JACKSON, 1978a) and her eggs. 5. A dead male of *M. niveus* was found in a web with another male. 6. A dead female of *M. niveus* was found in a web with a male. Each of these dead spiders had the appearance of eaten prey.

3. Methods for recording cannibalism.

An observation procedure was devised for comparing the cannibalistic tendences of different species. Cages were of the same design as those used for observations of spacing behavior. An adult female and two immatures (1 to 3^{mm} in body length) were placed into each cage. No flies were provided. Each cage had spiders of one species only. (Previous to these observations, each spider had been kept in an individual cage without food for 2 days.) For two days afterwards each cage was checked once in the early morning, once in the early afternoon, and once in the early evening (using a flashlight). Sixteen cages were set up for *M. gregalis* (communal, non-territorial species), 16 for *M. trivittatus* (communal, territorial), and 4 for *M. niveus* (solitary).

3. Results.

Two females of *M. trivittatus* were seen feeding on immatures. In another 7 cages one or two (one cage) immatures of *M. trivittatus* were found dead. Cannibalism seems likely in these cases since the carcasses had the appearance of eaten prey. In contrast, no deaths occurred for *M. gregalis* during the observation period. The frequencies of cages in which deaths of spiders occurred were significantly greater for *M. trivittatus* ($X^2=9.899$, $P(0.005$). Also, one of the cages of *M. niveus* had a dead immature, apparently having been preyed upon.

Discussion

I. Interspecific differences in courtship

The descriptions provided in this study should be viewed as a preliminary report, since there was considerable intraspecific variability and only a few interactions were observed for each species. In some animals there are elements of communicatory behavior that are used only infrequently, and a substantially more complete view of the species' communicatory behavior can be obtained by increasing observation time (ALTMANN, 1968; DANE and van der KLOOT, 1965; JACKSON, 1977b). However, with these limitations in mind, it would be valuable to compare the courtship of the three species observed in the laboratory in this study.

Abdomen twitching, and touching with face were of different form in each species. Interspecific differences in plucking and tapping silk, interplay of legs, pushing, and biting, although not clearly discerned, deserve further study. Jerk and quiver were observed in *M. trivittatus* only; rock in *D. calcarata* only; and pluck walk in *M. gregalis* only.

II. Elements of behavior in other species

Apparently, the elements of behavior observed for the species in this study are similar to those that occur during intraspecific interactions in other species of Dictynidae and species in the closely related family Amaurobiidae (BERLAND, 1916; BILLAUDELLE, 1957; BRISTOWE, 1958; GERHARDT, 1924; GREGG, 1961; LOCKET, 1926; McKEOWN, 1936; MONTGOMERY, 1903). However, since descriptions of spider courtship are generally lacking in detail, it is difficult to use the literature for comparative purposes.

III. The non-cannibalistic nature of *Mallos gregalis*

Mallos gregalis are non-cannibalistic despite seemingly ample opportunity. For example, when individuals arrived at a fly that was already covered by feeding spiders (fig. 10), they never inserted their fangs into a leg of another individual and treated a conspecific as prey. This would seem simple enough to do; and the cannibalistic individual would seem to benefit by gaining a meal and eliminating a competitor, which are important selection factors in some organisms (FOX, 1975). These observations raise the question of possible disadvantages for cannibalistic individuals. Perhaps cannibalism is selected against by kin selection (HAMILTON, 1964) or interdemic selection (WRIGHT, 1960). However, at this point we know almost nothing about the relatedness of individuals in natural populations or the rates of local population extinction for *M. gregalis*. More importantly, it is not clear that any of the characteristics, including the lack of cannibalism of these spiders require explanations outside the realm of individual selection.

Possibly there is a risk involved in making a predatory attack on another spider, since the attacked individual might injure or kill the attacking individual in the course of defending itself. Also the web is quite important in subduing prey (JACKSON, 1978d). Since *M. gregalis* do not become stuck in their own webs, another conspecific individual might constitute an especially difficult prey compared to a fly caught in the web. The energetic costs entailed in waiting for another fly caught in the web may be less than the costs, both in energy and risks, entailed in subduing another conspecific not caught in the web. This would be especially true if these spiders have substantial immunity to the venom of conspecifics, because in this case the bite would not quickly immobilize the victim. Since it seems unlikely that the attacked individual would remain stationary sufficiently long for the attaking spider to inject a great volume of venom, the venom would need to be rather effective. Physical restraint seems unlikely except for an adult attacking a very small immature, since immobilization wrapping (see ROBINSON, 1975) of prey does not occur in the Dictynidae, and these spiders do not seem to use their legs in holding prey (see ROVNER, 1978).

Although dead and not yet dried out individuals were seen at times in communal webs, feeding on these was never seen even though they were touched and walked over. Spiders will feed on dead, not yet dry, flies that they locate in the web. These observations raise the possibility that these spiders carry a toxin in their tissues that renders them noxious to other individuals. However, an immature *Phidippus audax* Hentz (Araneae, Salticidae) in the laboratory readily fed on *M. gregalis* taken from their web, providing no evidence that *M. gregalis* is protected by a toxin at least in the case of this predator. It is important to bear in mind the distinction between a toxin that might constitute a selection pressure against cannibalistic individuals and a chemical that serves solely as a signal (pheromone).

IV. The non-aggressive nature of *Mallos gregalis*

In general, speculations concerning the absence of cannibalism do not apply equally well to the absence of aggressive behavior.

One might predict that an individual who forces another away from a fly, at which there is no space to feed, would be at a selective advantage. However, conceivably the energetic costs and/or the risks of injury, if the opponent defends itself or escalates the intensity of the interaction (MAYNARD SMITH and PRICE, 1973), are greater than the costs involved in waiting for another fly.

In the laboratory, food was probably not limiting since the spiders were fed generously at frequent intervals; and this may be rather similar to the conditions in the spiders' natural habitats in Mexico during the rainy season. DIGUET (1915) and BURGESS (1976) made their observations in Mexico during the rainy season. What happens when the dry season arrives and food becomes less plentiful is unclear, since the few observations that have been carried out on this species in nature were mostly during the rainy season. The cost/benefit relations of spiders with respect to cannibalism and aggression would be expected to change with changes in the availability of prey. DIGUET's (1915) comments suggest that, at the end of the rainy season, some individuals disperse from the web and others remain at the web in a dormant state. We do not know whether aggressive and cannibalistic behavior occur with the arrival of the dry season, but there was no evidence of this in the webs kept in the laboratory without food for approximately a month. Since spiders are known to be adapted to endurance for extended periods without food (see ANDERSON, 1974; WITT, 1963), observations over a longer period of food deprivation would be valuable.

V. The function of courtship

If cannibalism reduction were the only function of courtship in dictynid spiders, then we would predict the absence of courtship in the non-cannibalistic species *M. gregalis* (see BURGESS, 1976). However, *M. gregalis* has distinct male courtship. If cannibalism reduction were a major but not exclusive function of male courtship, then we would predict less complex courtship in *M. gregalis*. A procedure of measuring complexity has not been devised for these spiders, although one approach might be to measure information content (SHANNON and WEAVER, 1949) with a larger number of observations. However, on the basis of the observations made in this study, differences among species in complexity are not evident. In each species there was repeated performance, in varied order, or a number of different signals.

If cannibalism reduction were a major function, then we would predict male courtship to have a "cautious" character in cannibalistic species, and we would predict *M. gregalis* courtship to be less cautious. The question of how to measure "caution" has not been dealt with, but various aspects of male courtship give an impression of caution in each species. For example, males frequently approached then withdrew from females, paused when the females began to walk, and moved their forelegs slowly and gently during interplay of legs. However, interspecific differences in caution were not evident.

GEIST (1971) pointed out that there is an alternative explanation for caution in male courtship for species in which males are not capable of physically restraining the female. Assume that the female will not mate until she has monitored some variable duration of male courtship. A male that attempts to mate, to approach closely, or to progress to a more advanced stage of courtship (contact phase, e.g., in dictynids) may force the female into making a "decision" as to whether she will permit copulation, proximity, etc. before it is optimal for her. Under these circumstances females may be very prone to simply decamp, ending the courtship interaction. A male that courts cautiously, hesitating when the female fails to respond, begins to decamp, or responds aggressively may be less likely to precipitate a premature departure by the female.

Another consideration is that cannibalism reduction lacks generality as a function of courtship in the animal kingdom, since highly complex courtship occurs in many groups in which cannibalism by the female would not seem to be a likely selection pressure on the males (e.g., *Drosophila*, SPIETH, 1974; grasshoppers, LOHER and CHANDRASHEKARAN, 1972; the ruff, RHIJN, 1973). This should caution us against underestimating the importance of functions other than cannibalism reduction for spider courtship. Certainly courtship might have multiple functions that differ in different groups of animals, and perhaps cannibalism reduction is an important function of courtship in some spiders. However, each case for which this is proposed should be critically investigated, and the primacy of this function for spiders in general is questionable.

What then are alternative functions that might be considered for animal courtship? No attempt will be made to review the extensive literature on this subject (see BASTOCK, 1967; MANNING, 1965; MORRIS, 1956). Instead, a few specific closing remarks will be made.

To say that the function of male courtship is to arouse the female or to bring her into readiness to mate does not completely answer the question, but shifts its focus: what is the function of a system in which females require male courtship before they are prepared to mate, or what is the function of female "coyness? " (RICHARDS, 1927; MANNING, 1966).

Two proposed functions have received particular emphasis. PECKHAM and PECKHAM (1889, 1890) argued for sexual selection by female choice in spiders. No data are available for the dictynids relevant to this hypothesis. Reproductive isolation has been emphasized as a function of animal courtship by DOBZHANSKY (1970), MAYR (1963), and others. Reproductive isolation would seem to present a potential problem for the dictynids in this study. Sometimes more than one species of the same genus were found in close proximity within the same habitat. For example, sometimes *M. niveus* were found on stems of the same trees on which there were *M. trivittatus* in web complexes around the trunk, as close as 1^m away. Also, the mating seasons of these two species overlapped. However, merely to point out interspecific differences in courtship behavior does not constitute adequate support of the hypothesis. Courtship between individuals of related species and female responses to experimentally manipulated signals (simulations of male vibratory signals using electronic transducers, alteration of male cheliceral shape, etc.) should be investigated. However, the most valuable approach would be comparative, looking at courtship in populations of the same species in which there are differing degrees of sympatry with related species. From the reproductive isolation hypothesis for the function of courtship, we would predict differences in courtship. The sexual selection hypothesis does not lead to this prediction.

Acknowledgements

For valuable discussions, I would like to thank P.N. WITT, M.C. VICK, S.E. SMITH, and J.W. BURGESS. Special thanks go to W.J. GERTSCH for his assistance in the identification of spiders and Lennell ALLEN for operating the electron microscope. C.E. GRISWOLD, P.S. JACKSON, and V.D. ROTH are gratefully acknowledged for helping me locate spiders in the field. The assistance of the Southwestern Research Station of the American Museum of Natural History is much appreciated. Thanks go to R.B. DANIELS, and T. MARSH for assistance with the manuscript. This work was supported in part by N.S.F. grant number BMS 75-09915 to P.N. WITT.

References

ANDERSON, J.F., 1974. – Responses to starvation in the spiders Lycosa lenta Hentz and Filistata hibernalis (Hentz). – *Ecology*, **55** : 576-585.

ALTMANN, S.A., 1968. – Primates, *in*: Animal communication (ed. T.A. SEBEOK), pp. 466-522. *Indiana University Press, Bloomington.*

BASTOCK, M., 1967. – Courtship: an ethological study. *Aldine, Chicago.*

BERLAND, J., 1916. – Note préliminaire sur le cribellum et le calamistrum des araignées cribellates et sur les moeurs des araignées. – *Arch. Zool. Expér. Gén.*, **55**: 53-66.

BILLAUDELLE, H., 1957. – Zur Biologie des Maurespinne Dictyna civica (H. Luc.) (Dictynidae, Araneidae). – *Z. Angew. Entomol.*, **41** : 474-512.

BRISTOWE, W.S., 1958. – The world of spiders. *Collins, London.*

BRISTOWE, W.S. & LOCKET, G.H., 1926. – The courtship of British lycosid spiders and its probable significance. – *Proc. Zool. Soc. London*, **1926** : 317-347.

BURGESS, W., 1976. – Social spiders. – *Sci. Amer.*, **234** : 101-106.

CHAMBERLIN, R.V. & GERTSCH, W.J., 1958. – The spider family Dictynidae in America north of Mexico. – *Bull. Amer. Mus. Nat. Hist.*, **116** : 1-152.

DANE, B. & van der KLOOT, W.G., 1965. – An analysis of the display of the goldeneye duck (Bucephala clangula (L.)). – *Behaviour*, **22** : 282-328.

DIGUET, L., 1915. – Nouvelles observations sur le mosquero ou nid d'araignées sociales. – *Bull. Soc. Acclim. France*, **62**: 240-249.

DOBZHANSKY, T., 1970. – Genetics of the evolutionary process. *Columbia University Press, New York.*

FOX, L.R., 1975. – Cannibalism in natural populations. – *Ann. Rev. Ecol. Syst.*, **6** : 87-106.

GEIST, V., 1971. – Mountain sheep: a study in behavior and evolution. *Chicago University Press, Chicago.*

GERHARDT, U., 1924. – Weitere Studien über die Biologie der Spinnen. – *Arch. Nuturg.*, **90** : 85-192.

GERHARDT, U. & KAESTNER, A., 1937. – Araneae, *in*: Handbuch der Zoologie, vol 3 (ed. W.G. KUKENTHAL), pp. 394-656. *DeGruyter, Berlin.*

GREGG, M., 1961. – The mating of Ixeuticus longinuus. – *Proc. Roy. Zool. Soc. New South Wales,* 1558-59 : 85-86.

GRISWOLD, C.E., 1977. – Biosystematics of Habronattus in California. M. Sc. Thesis, University of California, Berkeley.

GWINNER-HANKE, H., 1970. – Zum Verhalten zweire stridulierender Spinnen Steatoda bipunctata Linne und Teutana grossa Koch (Theridiidae, Araneae), unter besonderer Beruchsichtingung den Fortpflanzungverhaltens. – *Z. Tierpsychol.*, 27 : 649-678.

HAMILTON, W.D., 1964. – The genetical evolution of social behaviour. – *J. Theoret. Biol.*, 7 : 1-16.

HARRISON, J.B., 1969. – Acoustic behaviour of a wolf spider, Lycosa gulosa. – *Anim. Behav.*, 17 : 14-16.

HEDIGER, H., 1950. – Wild animals in captivity. *Butterworth, London.*

HUNTINGFORD, F.A., 1976. – The relationship between inter- and intraspecific aggression. – *Anim. Behav.*, 24 : 485-497.

JACKSON, R.R., 1974. – Rearing methods for spiders. – *J. Arach.*, 2 : 53-56.

JACKSON, R.R., 1977a. – Courtship versatility in the jumping spider, Phidippus johnsoni (Araneae: Salticidae). – *Anim. Behav.*, 25 : 953-957.

JACKSON, R.R., 1977b. – An analysis of alternative mating tactics of the jumping spider Phidippus johnsoni (Araneae, Salticidae). – *J. Arach.*, 5 : 185-230.

JACKSON, R.R., 1977c. – Comparative studies of Dictyna and Mallos (Araneae, Dictynidae): III. Prey and predatory behavior. – *Psyche* (in press).

JACKSON, R.R., 1978a. – Comparative studies of Dictyna and Mallos (Araneae, Dictynidae). I. Social organization and web characteristics. – *Revue Arachnologique,* 1 (4) : 133-164.

JACKSON, R.R., 1978b. – Male mating strategies of dictynid spiders with differing types of social organization. – *Symp. Zool. Soc. London,* 42 : 74-88.

JACKSON, R.R., 1978c. – Web sharing by males and females of dictynid spiders. – *Bull. British Arach. Soc.* (in press).

JACKSON, R.R., 1978d. – Predatory behavior of the social spider Mallos gregalis: Is it cooperative? (in review).

JACKSON, R.R. & SMITH, S.E., 1978. – Aggressions of Mallos and Dictyna (Araneae, Dictynidae): Population characteristics. – *Psyche* (in press).

KRAFFT, B., 1970. – Contribution à la biologie et à l'éthologie d'Agelena consociata Denis (Araignée sociale du Gabon). Première partie. – *Biol. Gabon.*, 6 : 199-301.

LEGENDRE, R., 1963. – L'audition et l'émission de sons chez les Aranéides. – *Ann. Biol.*, 2 : 371-390.

LOCKET, G.H., 1926. – Observations on the mating habits of some web-spinning spiders with corroborative notes by W.S. Bristowe. – *Proc. Zool. Soc. London,* 2 : 1.125-1.146.

LOHER, W. & CHANDRASHEKARAN, M.K., 1972. – Communicative behavior of the grasshopper Syrbula fuscovittata (Thomas) (Gomphocerinae) with particular consideration of the male courtship. – *Z. Tierpsychol.*, 31 : 78-97.

MANNING, A., 1965. – Drosophila and the evolution of behaviour. – *Viewpoints in Biology*, **4** : 125-169.

MANNING, A., 1966. – Sexual behaviour. – *Symp. Zool. Soc. London*, **3** : 59-68.

MAYNARD SMITH, J. & PRICE, G.R., 1973. – The logic of animal conflict. – *Nature*, **246** : 15-18.

MAYR, E., 1963. – Animal species and evolution. *Belknap, Cambridge, Mass.*

McKEOWN, K.C., 1936. – Spider wonders of Australia. *Angus and Robertson, Sydney.*

MONTGOMERY, T.H., 1903. – Studies on the habits of spiders, particularly those of the mating period. – *Proc. Acad. Nat. Sci. Philadelphia*, **55** : 59-149.

MORRIS, D.J., 1956. – The function and causation of courtship ceremonies. *In*: L'instinct dans le comportement des animaux et de l'homme (ed. P.P. GRASSÉ), pp. 261-287. *Masson et Cie, Paris.*

MOYER, K.E., 1968. – Kinds of aggression and their physiological basis. – *Comm. Behav. Biol.*, A, **2** : 65-87.

OTTE, D., 1974. – Effects and functions in the evolution of signaling systems. – *Ann. Rev. Ecol. Syst.*, **5** : 385-417.

PECKHAM, G.W. & PECKHAM, E.G., 1889. – Observations on sexual selection in spiders of the family Attidae. – *Occ. Pap. Wisconsin Nat. Hist. Soc.*, **1** : 3-60.

PECKHAM, G.W. & PECKHAM, E.G., 1890. – Additional observations on sexual selection in spiders of the family Attidae. – *Occ. Pap. Wisconsin Nat. Hist. Soc.*, **1**:117-151.

PLATNICK, N., 1971. – The evolution of courtship behaviour in spiders. – *Bull. British Arach. Soc.*, **2**: 40-47.

RHIJN, J.G. van, 1973. – Behavioural dimorphism in male ruffs Philomachus pugnax (L.) – *Behaviour*, **48** : 153-229.

RICHARDS, O.W., 1927. – Sexual selection and allied problems in the insects. – *Biol. Rev.*, **2** : 298-364.

ROBINSON, M.H., 1975. – The evolution of predatory behaviour in araneid spiders. *in*: Function and evolution in behaviour (eds. G. BAERENDS, C. BEER & A. MANNING), pp. 292-312. *Clarendon, Oxford.*

ROHLF, F.J. & SOKAL, R.R., 1969. – Statistical tables. *Freeman, San Francisco.*

ROVNER, J.S., 1978. – Adhesive hairs in spiders: behavioural functions and hydraulically mediated movement.– *Symp. Zool. Soc. London* (in press).

SAVORY, T.H., 1928. – The biology of spiders. *Sidgwick and Jackson, London.*

SHANNON, C.E. & WEAVER, W., 1949. – The mathematical theory of communication. *University of Illinois Press, Urbana.*

SOKAL, R.R. & ROHLF, F.J., 1969. – Biometry: the principles and practice of statistics in biological research. *Freeman, San Francisco.*

SPIETH, H.L., 1974. – Courtship behavior in Drosophila. – *Ann. Rev. Entomol.*, **19** : 385-405.

TURNBULL, A.L., 1973. – Ecology of the true spiders (Araneomorphae). – *Ann. Rev. Entomol.*, **18** : 305-348.

WILSON, E.O., 1975. – Sociobiology: the new synthesis. *Belknap, Cambridge, Mass.*

WITT, P.N., 1963. – Environment in relation to behavior of spiders. – *Arch. Environ. Health*, 7 : 4-12.

WITT, P.N., 1975. – The web as a means of communication. – *Biosci. Comm.*, 1: 7-23.

WRIGHT, S., 1960. – Physiological genetics, ecology of populations, and natural selection. *In*: Evolution after Darwin (ed. S. TAX), pp. 429-470. *University of Chicago Press, Chicago.*