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COMPARATIVE STUDIES OF *DICTYNA* AND *MALLOS* (ARANEAE, DICTYNIDAE): III. PREY AND PREDATORY BEHAVIOR

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INTRODUCTION

Although spiders are a major group of predaceous arthropods (see Turnbull, 1973), the types of prey consumed in their natural habitats are known for relatively few species. Some of the more noteworthy studies have employed daily monitoring of webs of araneids (Robinson and Robinson, 1970) and immunological techniques with lycosids (Greenstone, 1978); however, very little information is available for the dictynids. There is particular interest in the diet of dictynids because different species in this family live under a variety of types of social organization (Jackson, 1978). Discussions of the prime movers in the evolution of social phenomena frequently emphasize the type of prey taken by social predators (Wilson, 1975). An important factor for some species (e.g., army ants, canids, and killer whales) seems to be the ability of groups of individuals acting together to handle relatively large and dangerous prey. In order to evaluate the importance of this factor in the evolution of social phenomena in spiders, we need information concerning the diet and predatory behavior of species with differing types of social organization.

The species in this study belong to the closely related genera, *Mallos* and *Dictyna*. These are small cribellate spiders (body length usually 5 mm or less). Observations of actual feeding and other behavior related to predation were made in the western United States of America in June and July, and in south-central Mexico in September. Additional observations were made in the labora-

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tory. Also, arthropod carcasses in webs were collected and identified. Data are given as means ± S.D.

Most dictynid species are solitary, each individual generally living alone in an individual web that does not touch other occupied webs. Communal, territorial species (*M. trivittatus* Banks, *D. albopilosa* Franganillo, *D. calcarata* Banks) live in web complexes, consisting of web units connected to each other by silk. *M. gregalis* Simon (communal, non-territorial) lives in communal webs not subdivided into web units. Aggressive and cannibalistic behavior are virtually non-existent in this species, and individuals routinely feed in groups on the same prey. The other species are aggressive and cannibalistic, and most often they feed one spider per prey. In this paper basic information concerning the feeding behavior and diet of varied species will be presented, and a specific hypothesis will be discussed: namely, is predation on relatively large and dangerous prey an important factor in *M. gregalis?* Other aspects of the feeding behavior of *M. gregalis* have been reported elsewhere (Burgess, 1975; Jackson, 1979a; Witt, *et al.*, 1978).

Data concerning *M. gregalis* were gathered in conjunction with another study (Jackson, 1979a) to which the reader should refer for a description of laboratory methods. "Large webs" were communal webs built on plants in the laboratory, each probably containing several hundred spiders (Jackson and Smith, 1979); and these were not enclosed. "Small webs" (built by four spiders each) and "single-female webs" were built inside plastic cages. Data concerning where the spider first grasped the fly came from all three types of webs; data concerning size and composition of feeding groups came from large webs only.

Diet

Diptera were the predominant prey upon which *Dictyna* and *Mallos* were observed feeding (Table 1), and these dominated the collection of carcasses (Table 2). The data in Table 2 should be viewed as a list of probable rather than certain prey of these species, since some were possibly not fed upon by the dictynids. Two small Diptera in webs of *M. niveus* and one small Diptera in a web of *D. tridentata* were still filled with hemolymph. Probably these were captured flies on which the spiders had not yet fed completely. this species came from spending many hours observing a particular

Table 1. Number of instances of dictynids feeding on different types of prey listed according to their estimated relative sizes (prey size/spider size). When more than one individual fed on the same prey item (*M. trivittatus*), relative prey size based on largest spider.

Species	Type of Prey	Number of Prey			
		Smaller than Spider	Same size as Spider	Larger than Spider	Total
Dictyna calcarata	Diptera	0	1	2	3
Dictyna completa	Diptera	0	2	1	3
Dictyna phylax	Diptera	2	0	0	2
Dictyna tridentata	Diptera	1	1	0	2
Mallos dugesi	Diptera	0	1	0	1
Mallos niveus	Diptera	2	0	0	2
Mallos trivittatus	Diptera[a]	25	12	15	52
	Lepidoptera[b]	0	0	4	4
	Conspecific Spider	0	2	0	2

[a]Tipulidae: 14
Other Diptera: 38

[b]Moths

My approach to the web may have disturbed the spider, causing it to depart from the prey. A living tipulid caught in a *M. trivittatus* web will be discussed later. All other carcasses in Table 2 were dry, hollow, and almost entirely intact, which is the usual condition of prey of these spiders after feeding has occurred. Spiders inject enzymes into their prey, and digestion takes place primarily outside the spider's body. The spiders ingest the prey's tissues in fluid form. Unlike some other spiders, no noticeable mastication of the prey occurs with dictynids. Since other species of spiders (salticids, tetragnathids, etc.) frequently were found inside or near webs containing dictynids, possibly some of the arthropod carcasses in Table 2 were prey of these species, but most were probably prey of the dictynids. Predation on conspecifics (cannibalism) is discussed elsewhere (Jackson, 1979b).

Circadian Pattern of Feeding and Other Activities

Many more data are available concerning *M. trivittatus* than for the other species. Most of the observations of feeding (88%) for

Table 2. Number of arthropod carcasses ("prey remains") found in webs occupied by dictynids. Listed according to their estimated relative sizes (prey size/spider size). When more than one individual dictynid occupied the same web, relative prey size based on largest spider. Unidentified Dictyna: sp. no. 1, Querecho Plains, New Mexico, U.S.A.; sp. no. 2, Whiskey Mountain, Wyoming, U.S.A.; sp. no. 3, Lake Chapala, Jalisco and Michoacan, Mexico.

Species	Type of Prey	Number of Prey			
		Smaller than Spider	Same Size as Spider	Larger than Spider	Total
Dictyna albopilosa Franganillo	Diptera	8	5	2	15
Dictyna annexa	Diptera	30	16	1	47
Gertsch & Chamberlin	Coleoptera	0	1	0	1
Dictyna bellans	Diptera	2	2	0	4
Chamberlin	Lepidoptera[1]	0	0	1	1
Dictyna calcarata	Diptera	55	16	4	75
Banks	Coleoptera	0	2	2	4
	Homoptera[2]	2	0	0	2
	Hymenoptera[3]	0	2	0	2
	Lepidoptera[1]	0	0	1	1
Dictyna coloradensis	Diptera	21	1	2	24
Chamberlin	Hemiptera	0	0	1	1
Dictyna completa Chamberlin & Gertsch	Diptera	1	5	1	7
Dictyna tridentata	Diptera	42	46	37	125
Bishop & Rudeman	Coleoptera	0	0	1	1
	Hemiptera	0	0	1	1
Dictyna phylax Gertsch & Ivie	Diptera	9	3	0	12
Dictyna sp. no. 1	Diptera	26	7	0	33
	Hymenoptera[4]	0	0	1	1
	Lepidotera[1]	0	0	1	1
	Conspecific	1	0	0	1
Dictyna sp. no. 2	Diptera	0	4	4	8
	Hymenoptera[4]	0	0	1	1
Dictyna sp. no. 3	Diptera	7	8	6	21
	Homoptera[2]	1	0	0	1

Species	Type of Prey	Number of Prey			
		Smaller than Spider	Same Size as Spider	Larger than Spider	Total
Mallos dugesi Becker	Diptera	3	1	2	6
Mallos niveus	Diptera	57	38	18	113
O. P. Cambridge	Coleoptera	0	3	2	5
	Homoptera[2]	0	1	0	1
	Hymenoptera[4]	0	1	2	3
	Orthoptera[5]	0	0	1	1
	Thysanoptera	2	0	0	2
	Salticid spider	0	0	1	1
Mallos trivittatus	Diptera[6]	163	20	38	221
Banks	Coleoptera	1	0	0	1
	Homoptera[2]	3	0	0	3
	Hymenoptera[3]	1	0	0	1
	Lepidoptera	0	11	5	16
	Neuroptera	1	0	0	1
	Conspecific	2	3	0	5

[1]Moth
[2]Aphid
[3]Ant
[4]Wasp
[5]Grasshopper nymph
[6]Tipulidae: 33
Other Diptera: 188

web complex, located in a culvert through which a creek passed in the Chiracahua Mountains of Arizona. This large web complex was estimated to contain more than 10,000 individuals of *M. trivittatus* (Jackson and Smith, 1979). Since initial observations suggested that feeding occurred predominantly in the late afternoon and early evening (see below), one hour was spent inside the culvert on each of 12 evenings (5 in June; 7 in July); and records were kept for all observed cases of feeding. Diptera and other insects in the vicinity were especially active at this time of the day, and this was generally true in other habitats of *M. trivittatus* and the other dictynids.

Table 3. Temporal pattern of activity of spiders in their natural habitats. Time of day: early morning and early evening, within 2 hr before and after sunrise and sunset, respectively. Duration of observation estimated. Walking: without spinning and exclusive of intraspecific interactions. Intraspecific interactions described elsewhere. (Jackson, 1979b). *Dictyna phylax* and *Mallos dugesi* observed in day only.

Species	Time of Day	Duration of Observation (hr)	No of Spiders Feeding	No. of Spiders Walking	No. of Spiders Spinning	No. of Intraspecific Interactions
Dictyna calcarata	Early Morning	3	2	5	6	1
	Day	5	0	0	0	0
	Early Evening	2	1	0	0	0
Dictyna completa	Early Morning	2	1	0	0	0
	Day	4	2	0	0	0
	Early Evening	2	0	0	1	0
Dictyna phylax	Day	6	2	0	0	0
Dictyna tridentata	Early Morning	6	1	2	0	2
	Day	14	0	0	0	0
	Early Evening	4	1	0	0	0
Mallos dugesi	Day	7	1	0	0	0
Mallos niveus	Early Morning	5	0	0	0	0
	Day	14	2	0	0	0
	Early Evening	5	0	0	2	1
Mallos trivittatus	Early Morning	17	0	3	0	0
	Day	34	3	0	0	0
	Early Evening	19	53	18	3	9

With the exception of the evening observations in the culvert, the amount of time spent observing webs was recorded only approximately. These estimates were used for the calculations in Table 3. Based on these data, it seems that feeding and general activity of the dictynids in this study occur predominantly in the evening.

Initial Contact of Spider with Prey

Certain spiders, such as some araneids and theridiids, wrap their prey either before and/or after biting; however, this does not occur in the Dictynidae. These spiders seem to simply rush out and bite the prey. If the prey is violently struggling, the spider may walk or stand in the vicinity until activity subsides.

Bristowe (1958) reported that dictynids invariably grasp their prey initially by a leg. The initiation of feeding was seen for one *M. niveus* and five *M. trivittatus*. In each case, the spider initially grasped a leg or antenna of the prey. Of the spiders already feeding when found, some were feeding on the head, thorax, or abdomen of the prey (Fig. 1), although data were not recorded. *M. gregalis*, *M. trivittatus*, *M. niveus*, and *D. calcarata* were maintained and fed in the laboratory, and it was noted that the spiders sometimes initially grasped the prey by its head or body rather than by an appendage. For *M. gregalis* in the laboratory, the location at which the spider first grasped the prey was recorded for 66 individuals: leg, 44%; head, 15%; abdomen, 14%; thorax, 11%; wing, 9%; antenna, 7%. All of these flies were active when contacted.

Once I saw an opilionid walk onto a web unit containing an adult female *M. trivittatus*. The spider rushed out of its nest and grasped a leg of the opilionid with its chelicerae. Immediately, the spider released the opilionid and returned to its nest, suggestive of opilionids being distasteful to dictynids (see Bristowe, 1941). Several minutes later, the opilionid escaped from the web.

Extension Lines

Webs of *M. trivittatus* frequently contain long, heavy lines of silk (extension lines) that extend to objects some distance from the mesh (Jackson, 1978). Once in Utah I found an extension line fastened at one end to a mesh, with a female *M. trivittatus* inside the nest. On the other end, a tipulid fly was tethered by its thorax.

Fig. 1. Adult female *Mallos trivittatus* (body length: 7 mm) at East Turkey Creek (Chiracahua Mountains, Arizona) feeding on tipulid fly. Fly grasped at ventral thorax.

The tipulid flew in circles continuously for 10 min while I observed, after which I collected the fly and the spider. Of the set of *M. trivitattus* observed feeding in nature, 9% were on extension lines at the time; and 5% of the arthropod carcasses found in webs of *M. trivittatus* were found on extension lines. *M. gregalis* webs also have extension lines, and these spiders sometimes fed on flies caught on extension lines.

Feeding Groups — Size and Composition

The few cases in which more than one spider fed on the same prey in species other than *M. gregalis* are described elsewhere (Jackson, 1979b). In the laboratory, the size and composition of the group feeding on the fly was recorded 15 min after it contacted the web, and cases in which no spiders were feeding at the end of the 15 min are excluded. Group size was 4.8 ± 2.96 spiders (range: 1–15; $n = 38$). In the cases in which a single spider fed on the fly, three were females, two were immatures, and none were males. One of the immatures was a second instar; the other was almost adult size. In cases in which more than one spider fed on the fly, there were three groups consisting of females only; 4, immatures only; 21, females and immatures but no males; 2, males and immatures but no females; and 3, females, males, and immatures. In more casual observations, single males feeding on flies and groups consisting of females and males but no immatures were seen; but groups of more than one male but no females or immatures were not noticed. Groups of more than 20 individuals have been seen.

Discussion

Based on arthropod carcasses found in webs and observations of actual feeding in nature, Diptera seem to constitute the major prey of the closely related species of *Dictyna* and *Mallos* in this study. Billaudelle (1957), Bristowe (1958), and Wiehle (1953) commented on dictynids preying on Diptera, ants, and lice. Unfortunately, only limited information is available concerning the natural prey of *M. gregalis*, the communal, non-territorial species. I was not able to find this species when I was in Mexico. Diguet (1909a, b, 1915) and Burgess (1976 and personal communication) noted that Diptera seem to be the primary prey of this species in nature, although wasps are also fed upon. The Diptera seem to be predominantly ones of body lengths of approximately 5 to 10 mm, such as the "domestic fly" (presumably *Musca domestica*), tabanids, and bot flies. Burgess collected a portion of a web in Mexico; and when examined in the laboratory, it contained a great number of carcasses, all of Diptera in the size range of 5 to 10 mm. In the laboratory, *M. gregalis* has thrived for several years on a diet of *M. domestica* almost exclusively. The natives of Michoacan have

given this species the name *el mosquero*. During the rainy season, they take portions of communal webs from trees and place these in and around their homes, using them as fly traps (Berland, 1913; Diguet, 1909a, b, 1915; Gertsch, 1949).

Burgess (1975) has demonstrated that vibrations within a frequency range comparable to the wing beat frequency of *Musca domestica* is the most effective stimulus for eliciting predatory behavior from *M. gregalis*. Furthermore, the web transmits vibrations within this frequency range more readily than ones with other frequency characteristics. It seems that the web has characteristics that are particularly appropriate for the predominant prey species. The vibration transmission properties of webs of other species have not been investigated yet.

Some Diptera may be captured when they fly into *Dictyna* and *Mallos* webs. However, it was noticed that many Diptera tend to land on the stems and leaves of herbs and shrubs, on rock ledges, and on other objects on which dictynids tend to build their webs. Perhaps the majority of Diptera are captured when they inadvertently use a web as a perch. *Musca domestica* were frequently captured, seemingly in this manner, on webs of *M. gregalis* in the laboratory. These webs were kept in the open, on plants and other objects, in the laboratory. During routine feeding, house flies were thrown into the communal webs, but many inadvertently escaped into the room beforehand. Frequently these were seen subsequently landing on the webs and adhering to the silk. Thrown flies would seem more comparable to flying Diptera, and there is no evidence that the ratio of flies captured to ones that escaped differed for flies landing on the web compared to ones thrown into the web (Jackson, 1979a).

The extension lines in webs of *M. gregalis* and *M. trivittatus* may have a function related to predation. Diptera may find them to be particularly attractive perches and become trapped when they land on them. Another cribellate species, *Miagrammopes* (Uloboridae) has a single thread snare, and it reportedly captures Diptera that use the thread as a perch (Akerman, 1932).

Dictynid webs have nests, which are tubular structures of more densely woven silk; and the spiders tend to reside in their nests when not active. Spiders in various families (e.g., Agelenidae, Eresidae, Dysderidae) which have nests in their webs often transport prey to the nest before feeding(see Bristowe, 1958; Krafft, 1971). Araneid

spiders tend to transport prey to the hub of the web before feeding (Robinson and Olazarri, 1971). Although data were not collected, it was noticed that arthropod carcasses tended to be concentrated near the nests of the solitary and the communal, territorial species; and many of the feeding dictynids were near their nests at the time. These observations suggest that dictynids transport prey to their nests, although actual transport has not been seen. Billaudelle (1957) noted that *D. civica* carries prey from the periphery to the center of the web.

Most dictynid webs tend to be 2-dimensional; i.e., most of the silk of the web is in a single plane. In contrast, the communal webs of *M. gregalis* tend to be 3-dimensional; and the nests are in the interior of the webs, beneath the surface sheet on which flies are captured. Although flies were occasionally pulled into the interior of webs by spiders, in the vast majority of cases the prey was fed upon at the capture site in communal webs in the laboratory.

Returning to the hypothesis proposed at the beginning of this paper, is the prey of *M. gregalis* relatively large and dangerous compared to that of other dictynids? Diptera are apparently the primary prey of most species. Since Diptera such as muscids, culicidids, etc. would not seem especially dangerous for dictynids, differences in the danger associated with different prey would not seem important. Adult females of *M. gregalis*, the largest sex/age class, tend to weigh 4 to 21 mg, adult *Musca domestica* tend to weigh 10 to 20 mg (Witt, *et al.*, 1978). If prey of *M. gregalis* is in this weight range, then prey tends to range from approximately equal in size to individual spiders to a few times larger. In the solitary and in the communal, territorial species, prey were often smaller than the spiders. However, the difference in relative prey size among species is not absolute. Many prey of solitary and communal, territorial species were equal to or larger in size than the spiders (see also Bristowe, 1958; Wiehle, 1953).

Since prey sizes overlap for different dictynids, we need quantitative data from which variances can be calculated for relative prey size. Data from the natural habitats of *M. gregalis* in Mexico are especially needed. It will be tentatively concluded that *M. gregalis* preys primarily on relatively large prey. However, the differences in relative prey size do not seem dramatic. In a sense, the social organization of *M. gregalis* seems very different from that of the other dictynids, with great numbers of spiders living and feeding

together in the same communal webs. If diet is a major factor in the evolution of social phenomena in dictynid spiders, we might expect the diet of *M. gregalis* to differ greatly from that of other dictynids. Although differences in prey size seem to occur, perhaps the most interesting finding in this study is that there is considerable overlap in prey sizes of different dictynids. We need to consider the possibility that predation on relatively large and dangerous prey is only one among other equally or more important factors acting as prime movers in the evolution of social phenomena in the Dictynidae and perhaps for other groups as well.

Summary

Based on arthropod carcasses in webs and observations of actual feeding, Diptera seems to be the major prey of *Dictyna* and *Mallos*. *M. gregalis*, a species that routinely feeds in groups, may tend to prey upon relatively large prey compared to the other species. However, relative prey sizes overlap for species of all types of social organization. No apparent differences occur in the degree to which prey are dangerous. These observations are not to be expected from the hypothesis that the prime mover in the evolution of social phenomena in spiders is the ability of predators acting as a group to handle relatively large and dangerous prey. Although legs of flies are frequently grasped first, *M. gregalis* may initially grasp almost any part of the fly. Size of feeding groups varies greatly, ranging from 1 to more than 20. The hypothesis is proposed that prey is captured by *Dictyna* and *Mallos* primarily when flies use webs as resting sites. Feeding and other activity occur especially in the early evening and early morning.

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