

Web sharing by males and females of dictynid spiders

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Introduction

An important characteristic of most spiders that zoologists refer to as "social spiders" is that a group of conspecific individuals share a common web structure. The goal of this note is to present some observations concerning a particular type of web sharing in dictynid spiders, namely cohabitation by male-female pairs. Since a variety of types of social organization occur in the Dictynidae, this form of social behaviour is of particular interest in this group.

Solitary species

The majority of the dictynids seem to be solitary, constructing individual webs, usually occupied by a single individual. Each web consists of a mesh in which prey is captured and a nest (retreat) within the mesh in which the spider generally resides when not feeding or spinning. Only a single nest is found in each web. The webs of most of the solitary species in this study were found on stems and leaves of plants, although a few were on walls of buildings. These spiders tend to be aggressive and cannibalistic.

Communal and territorial species

Three species, *Mallos trivittatus* Banks, *Dictyna calcarata* Banks, and *D. albopilosa* Franganillo are communal, territorial. These spiders tend to be found in web complexes, consisting of a variable number of web units. Each unit consists of a nest and a mesh web, and it is connected to other units by strands of silk in the interstitial web. Since the mesh may be densely covered with silk, the term sheet web is often more appropriate. Each web unit may be occupied by a group of individuals, generally ones belonging to varied sex and age classes; and web units seem to be treated by these relatively aggressive and cannibalistic spiders as defended territories. Web complexes were

found on relatively flat surfaces such as walls of buildings and rock ledges (*M. trivittatus* and *D. calcarata*) or on herbaceous vegetation (*D. albopilosa*).

Communal and non-territorial species

Mallos gregalis Simon is a communal, non-territorial species. Large numbers of individuals intermingle without aggression or cannibalism in large communal webs. There are no defended territories as in web complexes. Some of the social characteristics of this species have been described by Digué (1915) and Burgess (1976), and this species is presently being investigated in the laboratory in North Carolina. One of the most important characteristics of *M. gregalis* is that groups of individuals of this species routinely feed simultaneously on the same prey. Group feeding is a comparatively rare occurrence in species with other types of social organization. The communal webs of *M. gregalis* are wrapped around leaves, stems, and branches of trees in Mexico.

Methods

Cohabitation will be defined here in a narrow sense to mean joint occupation of a web or web unit by an adult male and either an adult female or a female that will be mature after her next moult. These immatures will be referred to as "subadults". That those seen in nature were subadults was inferred from their large size and the fact that the outline of the epigynum could be seen under the cuticle when they were collected and later examined under the microscope.

Results

Altogether 17 species of solitary and 3 species of communal, territorial dictynids were observed in the field. Adult males were found for 9 of the solitary species and for all 3 of the communal, territorial species. These are listed in Table 1, along with records of cohabitation, the type of social organization adopted by each species, and the region in which the species was observed. This is only a preliminary list since merely a small fraction of this family, consisting of approximately 370 species (Chamberlin and Gertsch, 1958), was investigated. It seems very likely that, with additional observation, cohabitation will be

found to occur in additional species.

In some cases, both members of the cohabiting pair were inside the nest when they were found (Table 1). In the remaining cases, either the male and female were both outside the nest or only the female was inside the nest. In the case of two male/adult female pairs of *M. trivittatus*, two of *D. tridentata*, and one pair of *M. niveus*, the male was courting at the time of the observation. One pair of *M. niveus* were copulating at the time. In each other case, the spiders were inactive when observed, except for a pair of *M. trivittatus* that were feeding together on a tipulid fly. In the case of an adult female and male of *D. coloradensis* sharing the nest, a second male was in the mesh web, 5 cm away.

In *M. gregalis*, normally numerous adult males share large communal webs with large numbers of

adult females and immatures of all ages. Since systematic data were not taken, this species is not included in Table 1.

Discussion

Although cohabitation of adult males with adult females is known for many spiders (Bristowe, 1958; Jackson, 1976), both vagabond and web-building species, this phenomenon has not been studied in any depth for any group of spiders. Although it would be difficult to estimate exactly how widespread this phenomenon is, it seems safe to conclude that cohabitation does not occur in the majority of spiders. Both cohabitation and gregarious forms of social organization seem to be especially common in the Dictynidae. Perhaps the factors that favour both phenomena are

Species	Number of mature males found	Number of mature males found cohabiting with females		Social organization of the species	Localities (states) in which mature males were found
		Mature females	Subadult females		
<i>Dictyna albopilosa</i> Franganillo	5	2	1	Communal and Territorial	Morelos, Mexico
<i>Dictyna annexa</i> Gertsch and Mulaik	3	1	1	Solitary	New Mexico, U.S.A.
<i>Dictyna bellans</i> Chamberlin	1	0	0	Solitary	Colorado, U.S.A.
<i>Dictyna calcarata</i> Banks	16	6(1)	1	Communal and Territorial	Jalisco, Mexico
<i>Dictyna coloradensis</i> Chamberlin	3	2(1)	1	Solitary	New Mexico, U.S.A.
<i>Dictyna completa</i> Chamberlin and Gertsch	1	1	0	Solitary	Wyoming, U.S.A.
<i>Dictyna phylax</i> Gertsch and Ivie	3	1	2	Solitary	Wyoming, U.S.A.
<i>Dictyna tridentata</i> Bishop and Rudeman	11	4(1)	2(1)	Solitary	Colorado, Wyoming, U.S.A.
<i>Dictyna sp.</i>	3	0	0	Solitary	Morelos, Mexico
<i>Mallos dugesi</i> Becker	1	1	0	Solitary	Morelos, Mexico
<i>Mallos niveus</i> O.P.-Cambridge	21	7(4)	5(2)	Solitary	Arizona, Colorado, Utah, U.S.A.
<i>Mallos trivittatus</i> Banks	62	18(1)	4(1)	Communal and Territorial	Arizona, Colorado, Utah, U.S.A.

Table 1: Records of Cohabitation. The numbers in parentheses refer to cases in which males and females simultaneously occupied the same nest. The unidentified *Dictyna* is probably a new species. Localities in the United States were investigated during June and July, 1977; those in Mexico, September, 1977.

related, although at this stage of our knowledge the nature of these factors is unclear. One thing that both phenomena have in common is that they both involve sharing of web structures by more than one spider. Gertsch (1949) noted that males of dictynids are often seen living in webs of adult females, although he did not elaborate on the species involved. Bristowe (1958) noted that cohabitation with adult females occurs in some British dictynids, and sometimes the pair simultaneously share the same prey items. Both Bristowe and Gertsch noted that cohabitation may last for prolonged periods, although quantitative data from the field do not seem to be available. In some of the species listed in Table 1, perhaps prolonged associations do not occur, since the pairs might remain together only during courtship and copulation. We simply do not have adequate data upon which to base a conclusion at this time; but based on our knowledge of other spiders and the comments of Gertsch and Bristowe, prolonged association seems likely, especially in cases involving subadults.

Hopefully, the observations reported here will focus attention on the adaptive significance of cohabitation in Dictynidae and other spiders. Some possibilities that need to be considered will be mentioned in closing.

In a number of insect species, males remain with females and guard them from copulatory attempts by other males, either before or after the guarding male has copulated with the female (Parker, 1970). Sperm competition of this type seems to occur in linyphiid spiders (Rovner, 1968); and it needs to be investigated in other spiders, including the dictynids. Since laboratory studies have indicated that the females of at least some dictynid species will mate with more than one male (Jackson, unpublished data), there is the potential for sperm competition in the Dictynidae.

In the salticid spider *Phidippus johnsoni* Peckham and Peckham, adult males cohabit with subadult females and copulate when the female matures. In this case, cohabitation is a component of a complex mating strategy, in which males employ alternative tactics depending on the maturity and location of the female (Jackson, 1977). The time investment that the male makes in cohabiting is detracted from the time he could expend in searching for additional females. However, copulations that follow cohabitation differ

in important ways from other copulations by the same males in being longer in duration, more likely to lead to fertilized eggs, and more likely to result in the female being unreceptive to later males (Jackson, 1976). These observations raise the question of whether mating preceded by cohabitation with subadult females in dictynids differs in important ways in its consequences from other copulations, as it does in the salticid.

It is not known whether the male passively remains with the female or whether there is active communication involved in keeping the pair together. In certain birds and mammals, males and females may form pair bonds, which are defined in terms of individual recognition and the existence of categories of communication that are more or less restricted to pair members. As noted by Selander (1972), the widely used term "pair-bond" is difficult to define. The definition here corresponds roughly to that used by Hinde (1964). It would be of interest to explore the manner in which male-female pairs in spiders resemble pair bonding vertebrates. Another question of particular interest for the study of the evolution of social behaviour in dictynids is the question of whether the male and female interact in a cooperative manner. It is not known whether the male contributes to prey capture, web construction, and web repair.

Eventually we would like to understand the ultimate causes for patterns in Araneae with respect to cohabitation, including the question of why some species cohabit while others do not.

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References

- BURGESS, J. W. 1976: Social Spiders. *Scient.Am.* **234**: 101-106.
- BRISTOWE, W. S. 1958: *The World of Spiders*. London, Collins.
- CHAMBERLIN, R. V. and GERTSCH, W. J. 1958: The spider family Dictynidae in America north of Mexico. *Bull.Am.Mus.nat.Hist.* **116**: 1-152.
- DIGUET, L. 1915: Nouvelles observations sur le mosquero ou nid d'araignées sociales. *Bull.Soc.Acclim.Fr.* **62**: 240-249.
- GERTSCH, W. J. 1949: *American Spiders*. New York, D. Van Nostrand.
- HINDE, R. A. 1964: Pair formation, in A. L. Thompson (ed.), *A New Dictionary of Birds*. New York, McGraw Hill: 581-582.
- JACKSON, R. R. 1976: The evolution of courtship and mating tactics in a jumping spider, *Phidippus johnsoni* (Araneae, Salticidae). Ph.D. thesis, University of California, Berkeley.
- JACKSON, R. R. 1977: Courtship versatility in the jumping spider, *Phidippus johnsoni* (Araneae: Salticidae). *Anim.Behav.* **25**: 953-957.
- PARKER, G. A. 1970: Sperm competition and its evolutionary consequences in insects. *Biol.Rev.* **45**: 525-567.
- ROVNER, J. S. 1968: Territoriality in the sheet web spider *Linyphia triangularis* (Clerck) (Araneae: Linyphiidae). *Z. Tierpsychol.*, **25**: 232-242.
- SELANDER, R. K. 1972: Sexual selection and dimorphism in birds, in B. Campbell (ed.), *Sexual Selection and the Descent of Man*. Chicago, Aldine: 180-230.
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