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

I, social organization and web characteristics

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Contents

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Résumé

Les traits caractéristiques des toiles et les organisations sociales de 20 espèces ont été comparés dans la nature, et quatre au laboratoire. On trouve trois types de toiles et trois types correspondants d'organisation sociale. La plupart des espèces sont solitaires; trois espèces sont communales et territoriales (*D. albopilosa*, *D. calcarata*, *M. trivittatus*); et une espèce est communale, non-territoriale (*M. gregalis*). Les espèces solitaires vivent dans des toiles individuelles, chacune se composant d'un nid et d'un réseau. A l'exception des paires, mâle et femelle, et des femelles avec des enfants, on trouve une seule araignée par toile individuelle, et les toiles de ces espèces ne sont pas liées ordinairement aux autres toiles par de la soie. Les espèces communales et territoriales vivent dans des complexes de toiles, chacun se composant d'un nombre variable de toiles élémentaires (nid et réseau) qui sont liées les unes aux autres par une toile interstitielle. Chaque élément de toile a tendance à contenir un petit groupe d'araignées de classes de sexe ou d'âge différentes, et les occupants traitent les éléments de toile comme des territoires. Dans l'espèce communale non-territoriale, plusieurs milliers de toutes les classes de sexe et d'âge habitent des toiles communes qui ont des dimensions variables et qui ne se divisent pas en éléments de toiles défendus. Cette espèce se nourrit régulièrement en groupes sur une même proie. Ordinairement, les individus d'autres espèces se nourrissent isolément. Les sites des toiles varient à l'intérieur d'une même espèce, et les sites d'espèces d'organisation sociale différente s'interpénêtrent. Les emplacements des toiles sont la cause principale de leur forme. Beaucoup de débris peuvent s'accumuler dans les toiles de tous types. La compréhension des traits caractéristiques des toiles de *Dictynidae* semble être étroitement lié à la compréhension des types d'organisation sociale que l'on trouve chez ces espèces.

Summary

Web characteristics and social organisation of 20 species were compared in nature; four, in the laboratory. Three types of webs and three corresponding types of social organisation occur. Most species are solitary; three are communal, territorial (*D. albopilosa*, *D. calcarata*, *M. trivittatus*); and one is communal, non-territorial (*M. gregalis*). Solitary species live in individual webs, each consisting of a nest and a mesh. Except for male-female pairs and females with offspring, one finds a single spider per individual web, and the webs of these species are usually not connected to other webs by silk. Communal, territorial species live in web complexes, each consisting of a variable number of web units (nest and mesh or sheet) which are connected to each other by interstitial web. Each web unit tends to contain a small group of spiders of differing sex/age classes, and the occupants treat the web units as territories. In the communal, non-territorial species, up to several thousand individuals of all sex/age classes occupy communal webs, which are variable in size and which are not divided into defended web units. This species routinely feeds in groups on single prey items. Usually individuals of the other species feed alone. Web sites vary intraspecifically, and those of species with different types of social organisation overlap. Web sites are major determinants of web shape. Much debris may accumulate in webs of all types. Understanding dictynid web characteristics seems to be integral to understanding the types of social organisation found in these species.

INTRODUCTION

Although most spiders are "solitary" there are certain species that tend to live in groups, and some of these are referred to as "social spiders". The most extensively studied social species is *Agelena consociata* Denis (CHAUVIN and DENIS, 1965; DARCHEN, 1965, 1973, 1975, 1976; KRAFFT, 1969, 1970a, 1970b, 1971, 1975; PAIN, 1964). Some other important studies have dealt with the social characteristics of eresid (KULLMANN, 1969; KULLMANN *et al.*, 1972; KULLMANN and ZIMMERMANN, 1971), theridiid (BRACH, 1975, 1977; DARCHEN, 1968), and araneid (BLANKE, 1972; BUSKIRK, 1975; LUBIN, 1974) spiders. The *Dictynidae* are another group of spiders with social species. In particular, the Mexican species *Mallos gregalis* Simon lives in large communal webs in wich hundreds of individuals peacefully intermingle. DIGUET (1909 a, 1909 b, 1915), SEMICHON (1910), SIMON (1909) and BERLAND (1913, 1928) initially brought this species to the attention of scientific community, and BURGESS (1976) generated new interest. However, the social characteristics of other dictynid species have been largely neglected.

A group of dictynid species, *Mallos* and *Dictyna*, were chosen for this study because comments by CHAMBERLIN and GERTSCH (1958) suggested that closely related species in these genera vary extensively in their social characteristics. This opportunity for comparative studies would provide means of clarifying which characteristics of *M. gregalis* are adaptations related to social life. *Dictyna* is cosmopolitan in distribution. However, *Mallos* is restricted to a region extending from Central America north through the western parts of North America. Several months were spent in the summer of 1976 in Mexico and parts of the western United States (table 1), during which time data were collected for all species of *Mallos* and *Dictyna* that I could find in their natural habitats. Since the dictynids are web-building spiders and because web-spiders tend to be highly specialised in their adaptations related to life on a web (see PEAKALL, 1968, e.g.), a working hypothesis was that knowledge of the webs of these spiders would be integral to understanding their social organisation. Evidence of this will be presented.

WILSON (1971) proposed a logical sequence of four central questions in the study of social insects which might be profitably considered by students of social spiders. Paraphrasing WILSON, this paper will concentrate primarily on the first two questions: what are the qualities of social life in dictynid spiders, and how are dictynid "societies" organized? Questions concerning evolutionary steps and selection factors can be meaningfully investigated only after we have an understanding of social qualities and social organisation.

The group of spiders for which the expression "social" is used seems to be relatively clear. However, it is more problematical to provide definitions of spider sociality and categories of sociality because our knowledge of social phenomena in spiders is still in an early and changing stage (for reviews, see BURGESS, 1976, 1978; KRAFFT, 1970; KULLMANN, 1968, 1972; SHEAR, 1970). In the early development of a science, some terms need to remain flexible and be provided a chance to mature (BEER, 1977). This seems to be the case with the term "social" when applied to spiders. WILSON

NAME OF HABITAT	LOCATION	ELEVATION	WEB SITES	TERRAIN
Cuernavaca	Morelos, Mx. (in Cuernavaca)	1500 m	Buildings	
Guanajaato	Guanajaato, Mx. (in Guanajaato)	2000 m	buildings	
Juventinos Rosas	Guanajaato, Mx. (Juventinos Rosas)	2000 - 2500 m	Herbs, Shrubs	Flat
Lake Chapala	Jalisco & Michoacan, Mx.	1500 m		
1. Chapala	Jalisco (in Chapala)		Buildings	
2. Chula Vista	Jalisco (Chapala)		Herbs	Flat
3. Cojumatlan	Michoacan (Cojumatlan)		Herbs, shrubs	Flat
4. Ixtlahuacan	Jalisco (Ixtlahuacan de los Membrillos)		Shrubs	Gentle slope
Queretaro	Queretaro, Mx. (Queretaro)	2000 m	Herbs	Flat
San Anton Falls	Morelos, Mx. (Cuernavaca)	1500 m	Herbs	Very steep, slope (canyon walls)
San Miguel de Allende	Guanajaato, Mx. (in San Miguel de Allende)	2000 m	Buildings	
Bandelier	New Mexico, USA (Bandelier National Monument)	2000 m	Herbs, Shrubs	Flat

Table 1

NAME OF HABITAT	LOCATION	ELEVATION	WEB SITES	TERRAIN	PLANT COMMUNITY	BODIES OF WATER	NUMEROUS DIPTERA	TIME
Chiracahua Mountains	Arizona, USA						Various types, where water present. M and especially E	
1. Chiracahua National Monument	West side of range. (Chiracahua National Nomument)	2000 m	Shrubs	Flat, vicinity of dry creek bed	Similar to E. Turkey Creek			1,3 D
2. Cave Creek Canyon	East side of range (Portal)	1500 - 2000 m	Herbs, shrubs, rocks, boulders, buildings.	Flat or gentle slope	Similar to E. Turkey Creek	Sporadic in creeks		6,18 M,D,E
3. East Turkey Creek	East side of range (Portal)	2000 m	Herbs, shrubs, trees, rocks, boulders, culvert.	Gentle slope	a. Oak woodland b. Along creek, forest (canopy alternately open and closed) Alligator junipers[6].	a. Beside creek b. Inside metal culvert through which creek flows	Especially in culvert	14,48 M,D,E
4. Portal	East side of range. Base of mountains (Portal)	1500 m	Herbs, Shrubs, (especially *Gutierrezia*)	Flat	Desert, Mesquite[7]			5,9 D
5. Rustler's Park	East side of range (Portal)	2500 m	Herbs, rock ledges	Flat and gentle slopes	Similar to E. Turkey Creek			1,3 D
6. Winn Falls	East side of range (Portal)	2500 m	Rock ledge	Steep slope	Woodland. Walnut[8]	Ca. 100 m from creek and falls		1,2 D
Dinosaur	Utah, USA (Dinosaur National Monument)	1500 m	Shrubs	Flat	Desert, Sage[9] a. Thick growth of of sage[9] b. Scattered sage[9]	a. Beside green River b. Ca. 100 m from river		1,4 D
Flaming Gorge	Utah, USA (Flaming Gorge National Recreatior area)	2000 m	Trees, Rocks, Boulders	Gentle slope	Lodgepole pine[10] forest (closed canopy). Aspen[4].		Culicidae	2,3 M,E
Gila	New Mexico, USA (Gila Cliff Dwelling National Monument)	2000 m	Herbs, Shrubs	Flat	Scattered cottonwoods[4] and Junipers. Desert shrubs	a. Beside West Fork of Gila River b. Beside dry creek bed (no water in area)		1,3 D

NAME OF HABITAT	LOCATION	ELEVATION	WEB SITES	TERRAIN
Grand Teton	Wyoming, USA (in Grand Teton National Park) East side of Teton range			
1. Climber's Ranch	Jackson Hole	2000 m	Shrubs	Flat
2. Garnet Canyon	Just below timberline. Vicinity of Grand Teton	3000 m	Shrubs	Steep slopes
3. Leigh Lake	Jackson Hole	2000 m	Shrubs, trees	Flat
Guadalupe	Texas (in Guadalupe National Park) & New Mexico (in Carlsbad National Park) USA. East side of range		Shrubs	Flat
Querecho Plains	New Mexico, USA	1000 m	Shrubs	Flat
Rocky Mountain	Colorado, USA (Rocky Mountain National Park) East of park			
1. Big Thompson Canyon	(Loveland)	2000 m	Rock wall of canyon	Precipitous
2. Estes Park	(Estes Park)		Herbs, Rock ledge	Gentle slope
3. St. Vrain	North Branch of the St. Vrain creek	2500 - 3000 m	Shrubs	

NAME OF HABITAT	LOCATION	ELEVATION	WEB SITES	TERRAIN	PLANT COMMUNITY	BODIES OF WATER	NUMEROUS DIPTERA	TIME
Wind River Range	Wyoming, USA (Dubois)						Culicidae M,E	
1. Arrow Mountain	Above timberline	3500 m	Grass	Gentle slope	Short herbs	Melting snow		2,2 D
2. Big Meadows	Several meadows near Gannet Peak	3000 m	Shrubs	a. Flat b. steep slope	a. Meadow, thick growth of shrubs (willows[11]) b. Conifer forest	Beside Dinwoody Creek. Melting snow (especially in a)		4,9 M,D,E
3. Double Lake	Several lakes between Gannet Peak and Arrow Mountain	3000 m	Shrubs	Gentle and steep slopes	Conifer forest (alternately closed and open canopy)	Beside lakes, Melting snow		1,2 D
4. Gannet Tarn	Above timberline	3500 m	Shrubs	Gentle and steep slopes	Scattered short (<1 m) willow[11] shrubs			2,6 M,D,E
5. Ring Lake	Base of Whiskey Mountain	2000 m	Shrubs	Flat	Scattered timber pines[14], sage[9] and other shrubs	Beside lake		2,5 D,E
6. Whiskey Mountain[15]	Timberline	3500 m	Shrubs	Steep slope	Thick growth of willow[11] shrubs	Beside small stream created by melting snow		1,2 D

Table 1 - Description of habitats in which *Dictyna* and *Mallos* were studied. — Name of habitat: name (underlined), sometime abbreviated, of nearby distinctive geographical entity (city, mountain range, etc.) used for name of habitat. When useful to designate areas within the habitat, these are listed and numbered, but no underlined. — Location: State, country (Mx: Mexico; USA: United States of America). In parenthesis, name of geographical entity in vicinity ("in" when habitat is within the entity). — Elevation: Given to nearest 500 m. — Web sites: "Buildings", on outside walls of buildings. — Terrain and Plant community: no comments for habitats within cities. Dominant trees and shrubs mentioned when known. — Bodies of water and Numerous Diptera: noted when applicable. — Time: First, number of days; second, estimate for total number of hours spent searching, collecting, and/or studying dictynids in the habitat; M, D, E refer to times of day when habitats were visited; M, early morning (within few hr before and after sunrise); D, mid-day; E, late afternoon and early evening (within few hr before and after sunset).

Footnotes:

1: *Quercus* - 2: *Opuntia* - 3: *Atriplex canescens* - 4: *Populus* - 5: *Acer negundo* - 6: *Juniperus deppeana* 7: *Prosopis juliflora* - 8: *Juglans* - 9: *Artemisia* - 10: *Pinus contorta* - 11: *Salix* - 12: *Abies* - 13: *Picea* - 14: *Pinus flexipus* - 15: see JACKSON (1976) for more complete description.

(1975) takes a similar view concerning the term "society" when applied to animals in general. In this spirit, the term "social spider" will not be defined here. Instead it will be used as a rather general expression, the clarification of which is one of the ultimate goals toward which this study will hopefully contribute.

In the family *Dictynidae* there are approximately 350 described species in 34 genera (CHAMBERLIN and GERTSCH, 1958; for a different classification, see LEHTINEN, 1967), with species occuring in each of the major terrestrial biogeographical regions of the world. Numerous authors have provided information (predominately qualitative) concerning the webs and other aspects of the natural history of dictynids (BERLAND, 1916; BILLAUDELLE, 1957; BRISTOWE, 1941, 1958; CHAMBERLIN and GERTSCH, 1958; CLYNE, 1969; COMSTOCK, 1912; FORSTER and FORSTER, 1973; GERTSCH, 1949; KASTON, 1948; LOCKET and MILLIDGE, 1951; MAIN, 1971; MASCORD, 1970; McKEOWN, 1963; NIELSEN, 1931; WIEHLE, 1953; see above for references on *M. gregalis*). Based on this literature, it seems that the species in this study were rather representative for the family.

The dictynids are generally small in body size, and rather much intraspecific variation in body size was noted in this study (also see CHAMBERLIN and GERTSCH, 1958). Females of *M. trivittatus* tend to be 7 mm in body length, males, 5 mm. *Mallos* sp. (Lake Chapala) was of comparable size. *M. dugesi* females tend to be 5 mm, males, 4 mm. The remaining species tended to be less than 5 mm in body length.

TYPES OF WEBS AND SOCIAL ORGANISATION

Twenty species were studied in nature, and four were studied in the laboratory. From these data, three types of webs and three corresponding types of social organisation were identified (table 2 and 3).

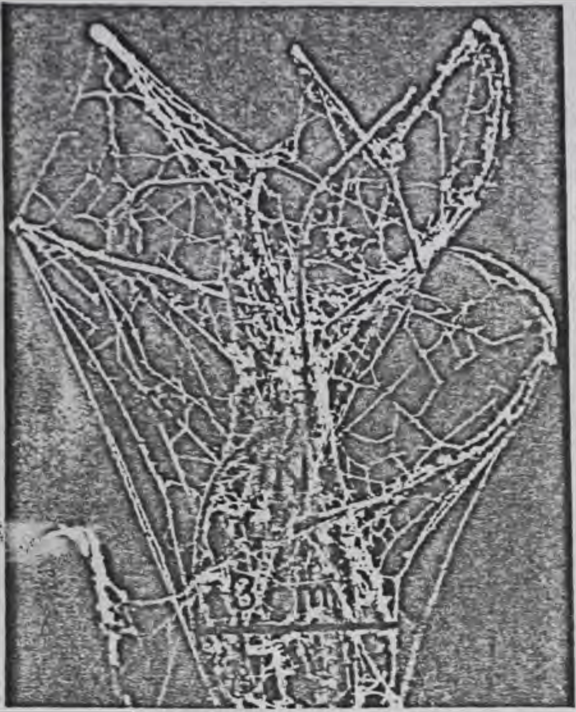
Individual webs. Solitary species.

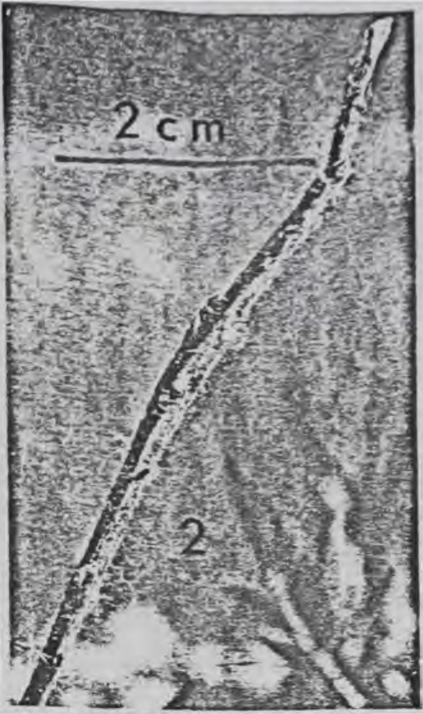
With a few exceptions that will be discussed later, solitary species occupied their webs singly; and these webs were rarely fastened to other webs. Typical individual webs are shown in fig. 1, 2 and 3. This type of web is the simplest, and the other types of webs can be described as elaborations upon the design of individual webs.

Type of social organisation	Solitary	Communal and territorial	Communal and non-territorial
Type of web	Individual	Web complex	Communal web
Components of web	Mesh, nest	Web units (mesh, nest) interstitial web	No web units
Number of spiders per web[1]	One	One or a small group	Hundreds
Feeding	One spider per prey	One spider per prey, occasionally in small group	Routinely in groups
Aggression and cannibalism	Yes	Yes	No

[1] Refers to web unit for communal and territorial species.

Table 2 — Characteristics correlated with different types of social organization.





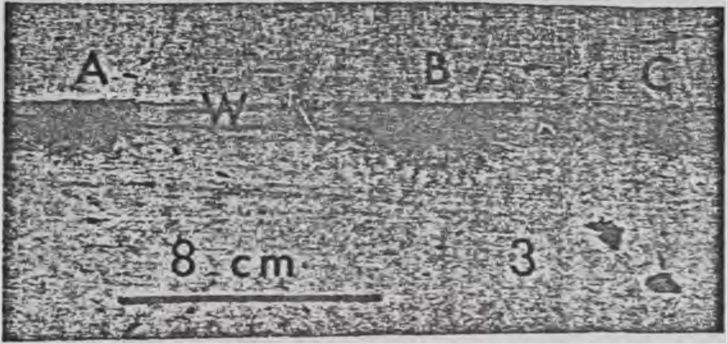


Figure 1 - Individual web of *M. niveus* on dry stem of herbaceous plant. M: mesh. Large, tubular nest (N) at junction of smaller stem with the primary stem (obscured by silk). *Toile individuelle de* M. niveus *sur une tige sèche de plante herbacée.* M: *réseau. Le nid* (N), *large et tubulaire, est à la jonction d'une petite tige sur la tige principale (caché par la soie).*

Figure 2 - Very narrow individual web of *M. niveus* on single dry stem of herbaceous plant. *Toile individuelle très étroite de* M. niveus *sur une simple tige sèche de plante herbacée.*

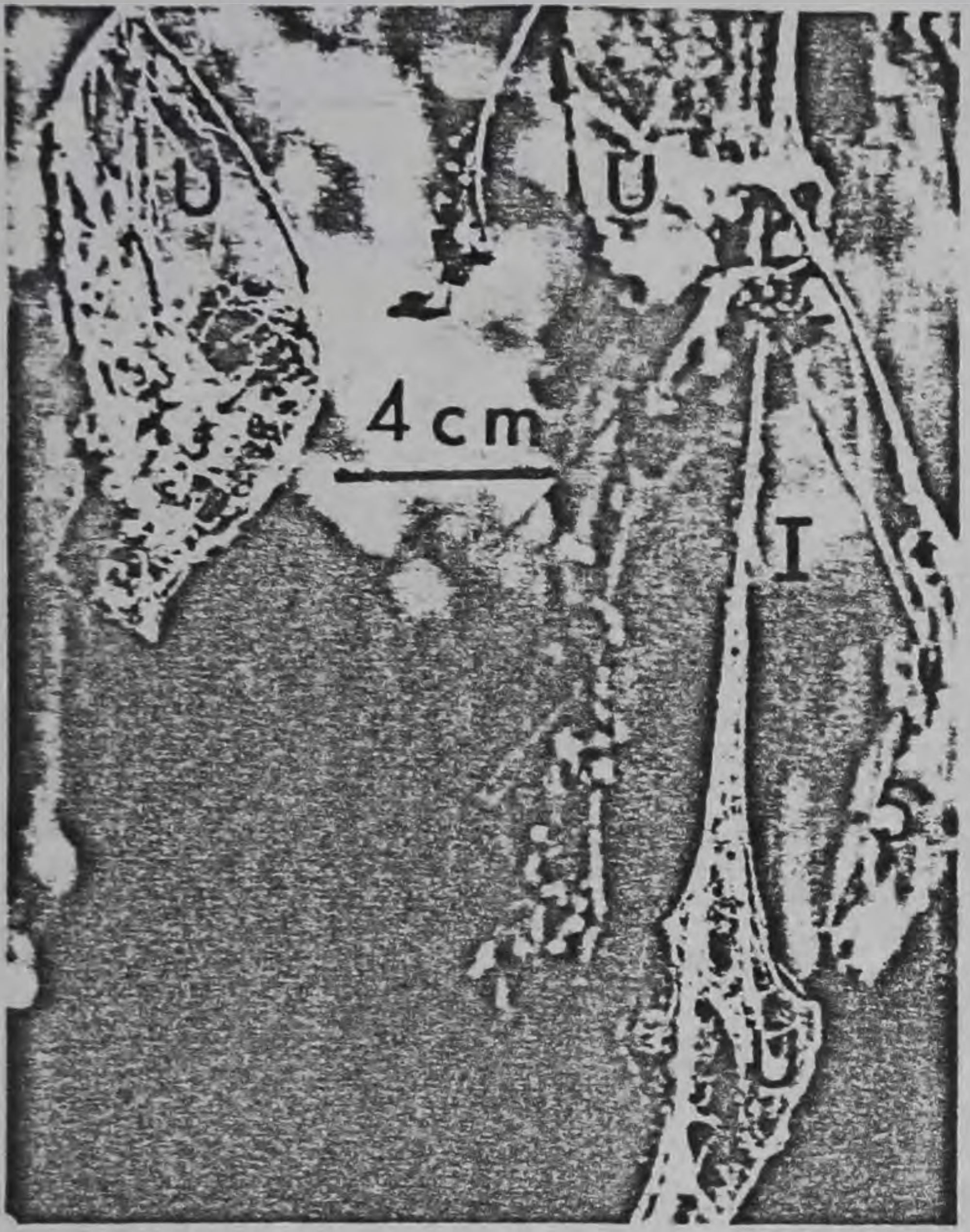
Figure 3 - Three individual webs (A,B,C) of *M. niveus* built partially in crevice on wall of building (W). *Trois toiles individuelles* (A,B,C) *de* M. niveus *construites partiellement sur une fente d'un mur de maison.*

Figure 4 - Diagram of web complex. M: mesh. N: nest. I: interstitial web. *Schéma d'un complexe de toiles.* M: *réseau.* N: *nid.* I: *soie intersticielle.*

Figure 5 - Part of web complex of *D. albopilosa* built on herbaceous plant. U: web unit. I: interstitial web. *Partie d'un complexe de toiles de* D. albopilosa *établi sur une plante herbacée.* U: *unité de toile.* I: *soie intersticielle.*

Figure 6 - Part of web complexe of *M. trivittatus*. Moss-covered rock (R) under overhanging, moss-covered rock ledge (L). Note: extension lines (E), some with cross-lines (C). Scale: ruler (lower right) 15 cm in length. *Partie d'un complexe de toiles de* M. trivittatus. *Rocher couvert de mousse* (R) *sous une saillie en surplomb couverte de mousse* (R). *Remarquez les prolongements de fils* (E), *certains avec fils transverses* (C). *Echelle: la règle, en bas à droite, mesure 15 cm.*

Figure 7 - Communal web of *M. gregalis* on philodendron plant growing in flower pot (P). Note fly carcasses (F) in web and leaf covered by relatively little web (L). *Toile commune de* M. gregalis *sur un "philodendron" poussant dans un pot* (P). *Remarquez les carcasses de mouches* (F) *sur la toile et la feuille couverte d'une relativement petite toile.*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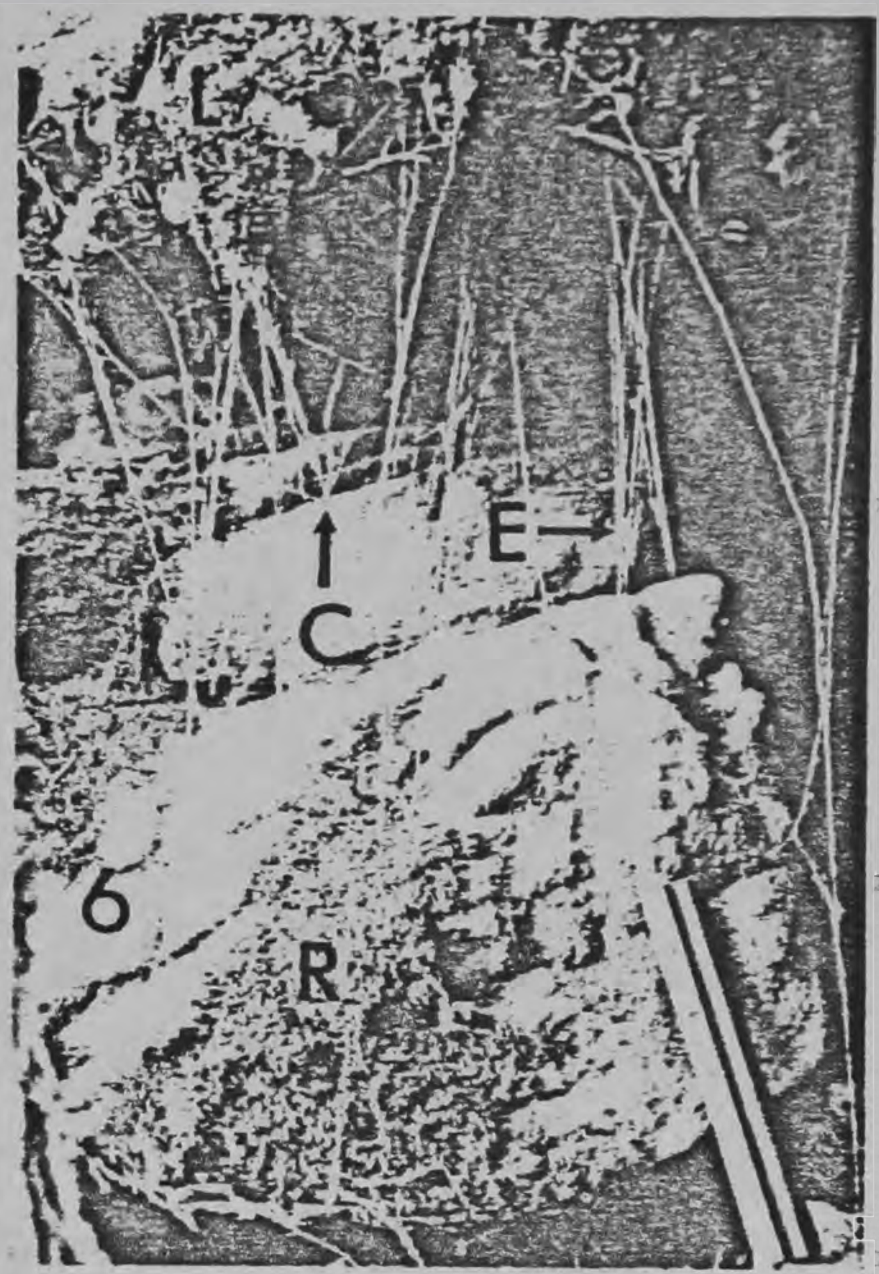
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Web complexes. Communal, territorial species.

One can visualize a web complex as the result of placing individual webs in close proximity and connecting them by silk in the interstitial area (fig. 4, 5 and 6). The number of units in a single web complex is highly variable. For each species, two was the minimum. Approximately 6 500 was the maximum for *M. trivittatus*; 19 for *D. calcarata*; and 24 for *D. albopilosa*.

Communal webs. Communal, non-territorial species.

M. gregalis envelopes leaves, stems and sometimes whole branches of trees (*Acacia*, *Quercus*, etc.) in Mexico in large sheet webs. As noted by DIGUET (1909a, 1909b), the over-all appearance is rather like that of the webs of tent caterpillars (fig. 7). The "surface sheet" (BURGESS, 1976) is perforated with holes that lead into the interior of the web. Under the sheet there are various sizes of "chambers", similar to the nests of other dictynids, and long tunnels, sometimes more than 10 cm in length. Also there is a meshwork of "supporting lines" that connects the surface sheet with the twigs, leaves, and other substrates beneath. The spiders reside in the chambers much on the time, and egg sacs are placed here.

Territoriality.

WILSON's (1975) definition of territory will be used: "an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defense or advertisement." Animal territories may be defended against other species, conspecific individuals only, or against only certain sex/age classes of conspecifics. In the dictynid species that live in web complexes, web units seem to be territories that large individuals defend against other individuals of comparable size. Patterns of feeding, aggression and cannibalism are consistent with territorial behavior in these species and non-territorial behavior in *M. gregalis*, as will be discussed later.

WEB SITES

Considering the species in this study (table 3) and reports from the literature for other species, a wide variety of web sites are used by dictynid spiders; and there can be considerable intraspecific variability. Also, the type of web sites used by solitary and communal species overlap. The greatest variability was recorded for the species observed most extensively in nature (table 1 and 3), *M. niveus* and *M. trivittatus*, suggesting that greater variability for other species would be revealed if observation time were increased. In particular, we might expect more variability for *M. gregalis* in Mexico, since in the laboratory communal webs enveloped stems and leaves of living plants, as well as numerous other objects such as table tops, corners of the room, and light fixatures. Data from the natural hatitats of this species are much needed.

SPECIES	SOCIAL ORGANISATION	DISTRIBUTION	HABITATS	WEB SITES
Mallos dugesi Becker	Solitary	Southwestern USA, western and southern Mexico	San Anton Falls	Herbs (21)
Mallos niveus O.P. Cambridge	Solitary	Western USA, Mexico, Guatemala	Guanajaato, Queretaro, Chiracahua Mountains (1,2,3), Dinosaur, Rocky Mountain (1)	Herbs (76), shrubs (29), trees (1), buildings (48)
Mallos pallidus Banks	Solitary	Western USA, northern Mexico	Lake Chapala (2)	Herbs (2)
Mallos sp.	Solitary		Lake Chapala (3,4)	Herbs (4), shrubs (10)
Dictyna annexa Gertsch & Chamberlin	Solitary	Texas, New Mexico, adjacent Mexico	Juventinos Rosas, Gila, Guadalupe Mountains	Herbs (10), shrubs (12)
Dictyna annulipes Blackwall	Solitary	Holarctic	Wind River Range (5)	Shrubs (10)
Dictyna bellans Chamberlin	Solitary	Central USA as far west as Utah and Arizona, Mexico	Rocky mountain (1)	Herbs (4)
Dictyna coloradensis Chamberlin	Solitary	Canada, northern USA, Rocky Mountains and adjacent Great Plains	Bandelier, Wind River Range (5)	Shrubs (10)
Dictyna completa Chamberlin & Gertsch	Solitary	Western USA	Wind River Range (1,4)	Shrubs (14)
Dictyna peon Chamberlin & Gertsch	Solitary	Southern Arizona and New Mexico, Mexico	Chiracahua Mountains (5)	Herbs (1)
Dictyna phylax Getsch & Ivie	Solitary	Canada, northern USA	Grand Teton (3), Rocky Mountain (3)	Herbs (2) shrubs (2) trees (36)
Dictyna tridentata Bishop & Rudeman	Solitary	Rocky Mountains south into Mexico	Grand Teton (1,2,3), Rocky Mountain (2) Wind River Range (2,3)	Herbs (9), shrubs (32)
Dictyna tucsona Chamberlin	Solitary	Southwestern USA, Mexico	Chiracahua Mountain (4)	Herbs (1), shrubs (14)
Dictyna sp.	Solitary		Chiracahua Mountains (2)	Herbs (3)
Dictyna sp.	Solitary		Querecho Plains	Shrubs (20)
Dictyna sp.	Solitary		Wind River Range (6)	Shrubs (10)
Dictyna sp.	Solitary		San Anton Falls	Partially folded leaves of herbs (21)
Mallos trivittatus Banks	Communal and territorial	Western USA, northern Mexico	Chiracahua Mountains (2,3,5,6) Flaming Gorge, Rocky Mountain (1,2)	Metal culvert (ca.6 500), boulders (16), large rocks (48) rock ledges (85), trees (41) buildings (1)
Dictyna albopilosa Franganillo	Communal and territorial	Mexico, Cuba	San Anton Falls	Herbs (77), buildings (16)
Dictyna calcarata Banks	Communal and territorial	Western USA, Mexico	Lake Chapala (1), San Miguel de Allende	Buildings (128)

Table 3 - Dictynid species observed in nature. Distribution from CHAMBERLIN and GERTSCH (1958). Habitats refer to the specific locations at which found each species in this study. Numbers in parentheses refer to areas within habitats (see table 1). Number of occupied webs found at each type of web site listed in parentheses.

A single occupied web of *M. niveus* was found on a dead stem of an oak tree (table 3) in the Chiracahua Mountains (E. Turkey Creek). However, several empty webs, similar to this one, were found on dead stems of other oak trees in the area, suggesting that although construction of webs on trees may be less common than on shrubs and herbaceous plants, it is nevertheless characteristic of this species.

The only other solitary species that was found on trees was *D. phylax* which built webs on green stems and needles of spruce (*Picea*) and fir (*Abies*) trees. Perhaps this species has a preference for conifer trees, but this needs further investigation.

Another possible example of web site specificity is *Dictyna* sp. (San Anton Falls), all webs of wich were on the upper surface of green leaves. In every case, each outer edge of the leaf parallel to the central axis of the stem was rolled somewhat upward, and the webs were spun across the basin made by the curvature of the leaf. Similar webs have been described for other dictynids (e.g. BERLAND, 1916; WIEHLE, 1953).

With the exception of *D. phylax* and *Dictyna* sp. (San Anton Falls), when individual webs were located on plants they were especially prone to be found on dry, dead stems. Of the 172 webs for which data were gathered (see table 4 for sample sizes for each species, excluding *D. phylax* and *Dictyna* sp.), 81.98 % were entirely on dry stems, 15.12 % were entirely on green stems, and 2.91 % were partially on green and partially on dry stems. It would be valuable to investigate whether these spiders are actively choosing dry stems for web sites.

On occupied web (Arrow Mountain; *D. completa*), containing a male-female pair, was fastened to a blade of grass and to two adjacent rocks. The grass blade extended 6 cm above the ground, and the web was oriented vertically along the grass and extended to the tip of the blade. The nest and the spiders were in the lower part of the web beside a rock. This was the only web of any species found on a blade of grass in this study.

Individual webs on shrubs, trees, and herbaceous plants were usually constructed near the tips of the stems. The mean distance from the distal end of the web to the stem tip was 0.9 cm (see table 4 for sample sizes for each species). The maxima were 30 cm for one *M. niveus* web on a shrub and 25 cm for a web of *D. phylax* on a fir tree; 86.67% of the webs extended to within 0.5 cm of the stem tip.

The distance above the ground was rather variable, but generally it was less for herbs than for shrubs (table 5). Shrubs were generally taller than herbs, and webs were usually constructed near the tops of herbs and shrubs. Although trees were not searched at heights much greater than 2 m, dictynid webs at Leigh Lake could be seen more than 3 m above the ground; and it seems likely that dictynid webs on trees occur at even greater distances above the ground.

GEOGRAPHICAL DISTRIBUTION AND HABITATS

Communal, territorial and solitary species were both found in temperate as well as tropical regions. The only communal, non-territorial species seems to be restricted to a tropical region with distinct rainy and

S[illegible]ES	NUMBER OF WEBS MEASURED	LENGTH	WIDTH	DEPTH	ROUDNESS	STEM DIAMETER	SURFACE AREA
M. niveus A	29	4.5±2.01	2.7±1.20	0.0±0.00	0.6±0.10	no stem	12.1
M. niveus B	1	12	4	2	0.3	2	48.0
M. niveus C	69	12.3±5.47	2.6±1.29	0.3±0.63	0.3±0.16	1.0±0.54	32.0
M. pallidus	2	13, 8	2, 2	0, 0	0.1, 0.3	0, 0	21.0
M. trivittatus	42	5.0±1.48	4.2±0.96	0.0±0.00	0.9±0.16	no stem	21.0
Mallos sp. (Lake Chapala)	8	12.6±3.70	3.4±2.56	0.3±0.46	0.3±0.26	0.9±0.35	42.8
D. annexa	16	10.9±4.69	3.9±4.01	0.4±1.03	0.3±0.20	0.9±0.57	42.5
D. annulipes	10	9.4±3.17	2.0±1.41	0.1±0.32	0.2±0.16	1.2±0.42	18.8
D. calcarata	26	2.5±1.57	1.8±0.89	0.0±0.00	0.8±0.22	no stem	4.5
D. coloradensis	10	11.1±3.14	4.0±2.63	0.9±1.60	0.4±0.18	0.7±0.48	44.4
D. completa	8	6.5±1.19	3.5±0.76	0.6±0.52	0.5±0.07	0.7±0.46	22.7
D. phylax	8	9.5±4.00	3.4±1.77	0.1±0.35	0.4±0.17	1.5±0.54	32.3
D. tridentata	31	8.5±2.89	4.3±2.87	0.3±0.46	0.5±0.28	1.1±0.51	36.5
D. tuscona	7	3.7±1.50	1.4±0.79	0.0±0.00	0.4±0.13	0.7±0.49	5.2
Dictyna sp. (Querecho Plains)	11	11.1±2.85	3.5±1.13	0.3±0.47	0.3±0.15	1.2±0.41	38.9

Table 4 - Web characteristics. *M. trivittatus* and *D. calcarata*: web units from web complexes (see table 2), all on relatively flat surfaces. All other species: solitary. *D. phylax*: webs on conifer trees. *M. niveus* A: on walls of buildings. *M. niveus* B: on oak tree. All other individual webs: on herbs and shrubs. Length, width, and depth defined in text. Roundness: width divided by length. Stem diameter at widest point on primary stem (see text) within web. All measurements accurate to the nearest cm except stem diameter (nearest mm). All measurements made on occupied webs. Means only provided for surface area (mean length x mean width). Other characteristics: means ± S.D., except for *M. niveus* B and *D. pallidus* for which actual measurements are provided.

SPECIES	WEBS SITES	NUMBER OF WEBS MEASURED	DISTANCE
M. niveus	Herbs	51	60 ± 27.1
	Shrubs	18	112 ± 43.9
	Trees	1	145
M. pallidus	Herbs	2	90, 60
Mallos sp. (Lake Chapala)	Herbs	1	60
	Shrubs	7	75 ± 37.8
D. annexa	Herbs	10	66 ± 27.6
	Shrubs	6	105 ± 16.4
D. annulipes	Shrubs	10	99 ± 28.5
D. coloradensis	Shrubs	10	47 ± 11.3
D. completa	Shrubs	8	35 ± 17.7
D. phylax	Shrubs	2	130, 65
	Trees	6	160 ± 24.5
D. tridentata	Herbs	7	52 ± 10.4
	Shrubs	24	105 ± 26.5
D. tucsona	Herbs	1	35
	Shrubs	6	55 ± 12.2
Dictyna sp. (Querecho Plains)	Shrubs	11	62 ± 24.9
Dictyna sp. (Wind River Range)	Grass Blade	1	1

Table 5 – Distances above the ground from proximal edge of web, solitary species. Measured to nearest 5 cm, except for *Dictyna* sp. (Wind River Range) which was measured to nearest 1 cm. When N = 1 or 2, actual distances instead of means provided.

dry seasons. Generally there was considerable intraspecific variability in the types of habitats occupied (see table 1 and 3). *M. niveus*, for example, was found from desert habitats (Dinosaur) to relatively mesic habitats (e.g., Big Thompson Creek). *D. tuscona*, another solitary species, seems to be restricted to desert habitats, judging from collection sites listed by CHAMBERLIN and GERTSCH (1958) and the fact that all those found in this study were from desert habitats. None of the communal species were found in desert habitats.

WEB SIZE AND GEOMETRY

Individual webs.

Webs built on stems of plants will be considered first. In these the mesh is an array of silk lines with many relatively large gaps between threads. The spatial relationship of threads has not been quantitatively determined, but it would seem rather irregular, at least when compared to a web such as that of *Araneus diadematus* Clerck (*Araneidae*) which has consistent, regular symetry (WITT, REED and PEAKALL, 1968).

The shapes of webs are to a large extent correlated with the characteristics of the stems around which they are spun. This contrasts with the orb webs of araneid spiders, for exemple, in which shape is nearly independent of the substrate on which webs are spun (BURGESS and WITT, 1976). Often there was one stem with distinctly greater thickness (primary stem) to which individual dictynid webs were fastened at numerous points. Threads were frequently fastened to smaller side branches as well. The primary stem usually was not much more than 1 mm in diameter (table 4). On shrubs there were always numerous stems present with greater diameter than the primary stem. However, the primary stem was frequently the largest stem on herbaceous plants.

The longest distance across the web (length) was more or less parallel to the primary stem in almost every instance. The length of the web was oriented most nearly vertically in 91.35 % of the 185 webs sampled (see table 4 for sample sizes for each species), and most nearly horizontally in 7.03%. The longest axis of one web was not oriented clearly in either the vertical or horizontal plane; and in another two, one axis was not clearly of greater extent than the other. Width is defined as the second greatest distance across the web on an axis perpendicular to the length. When a third axis is imagined perpendicular to the plane containing the length and width, the greatest distance across the web in this axis is defined as the depth.

For most webs length was 10 to 12 cm, width was only a few centimeters, and depth was less than 1 cm (table 4). In other words, webs tended to be two-dimensional in the sense that most of the silk lay in one plane. In a few cases, depth was nearly as great as the width. However, even in these cases, the web was two-dimensional in a sense. Lines of silk were laid from the heavy central stem out to side stems; and in most webs this was primarly to stems in a single plane approximately perpendicular to the length and width of the web. In effect, these webs consisted of two sections, each perpendicular to the other. Few if any threads tended to go from one section to the other, except in the vicinity of the central stem.

The webs of *M. niveus* built on walls of buildings were similar in basic respects to those on vegetation. Each had a nest and a mesh with a lattice-work appearance. However, these webs, set flat against the wall, were almost entirely two-dimensional. The nest was always near the center of the web. Usually the shape of the web approached that of a circle. Compared to webs on vegetation (table 4), length was less ($t = 7.093$, $P < 0.001$), perhaps reflecting a tendency to concentrate silk within a shorter distance from the nest when the substrate is more uniform. On vegetation, features of web site, such as the distance to branching stems, may have a greater influence on web length. If this is the case, on might also predict greater roundness of webs on walls; however, the differences in table 4 were not significant (t-test).

Measurements were not made on webs built across concavities of leaves (*Dictyna* sp., San Anton Falls), but these webs were estimated to be generally 3 cm long and 2 cm wide, usually approximately half the size of the leaf.

In conclusion, individual webs of species in this study were rather similar in size and structure, and geometry varied more with the nature of the web site than with the species.

Web complexes.

In the Chiracahua Mountains there was an enormous web complex (estimated surface area: 79 m^2) in the metal culvert on East Turkey Creek, estimated to coutain 6,500 occupied web units and 10,200 individuals of *M. trivittatus* and covering almost the entire interior surface of the culvert (JACKSON and SMITH, 1978). Web complexes of *D. calcarata* and *D. albopilosa* and other web complexes of *M. trivittatus* were considerably smaller, tending to be more or less 1 m^2 in surface area.

Unlike the web complexes of the other two species, those of *D. albopilosa* were three-dimensional, since they were wrapped around leaves and stems in dense growth of herbaceous plants (fig. 5). Detailed data concerning these web complexes were not collected because of the difficulty of dissecting the web units. However, most web complexes seemingly consisted of a dozen or so units. Stem (0.67 ± 0.594 cm) and leaf diameter (5.56 ± 1.120 cm) were measured for 19 plants that supported web complexes. Most webs were wrapped around green leaves, although some were on dry ones. These plants grew on the nearly vertical cliffs beside San Anton Falls, In some places, dirt had fallen away exposing roots of these plants, and some web complexes were on the roots. Each web unit tended to be approximately 10 cm x 5 cm; however, the boundaries between units were often difficult to distinguish. In some cases, an area of 400 cm^2 or more was almost completely covered with silk. More commonly, there was a patchwork of areas alternatively covered and not covered by silk. The density of silk in these webs was great in most cases, concealing the spiders and the underlying vegetation. In some cases, careful examination revealed nests; and these tended to be near the center of the web units.

Communal webs.

Communal webs of *M. gregalis* in Mexico were variable in surface area sometimes covering many square meters (DIGUET, 1909a, 1909b, 1915; BURGESS, 1976). The number of spiders per web varied greatly in nature and the laboratory. Probably as many as 20,000 share single communal webs at times in nature (JACKSON and SMITH, 1978).

EXTENSION LINES

Webs of *M. trivittatus* frequently had extension lines (fig. 6), which are heavy lines composed of multiple threads that extend from the mesh to an object some distance away. Of 92 sampled web units, 30.43% had extension lines. Excluding those without extension lines, there were 1.2 ± 0.50 extension lines per web unit, each 18.6 ± 9.62 cm in length. Similar lines were seen in the communal webs of *M. gregalis*, extending from one communal web or portion of a web to another or to an external object. Extension lines were not found on webs of ather species. Potential functions of these in prey capture have been proposed (JACKSON, 1978a).

DEBRIS AND PREY REMAINS IN WEBS

As noted by other authors, dictynid webs were often covered by considerable amounts of dust and other debris. For example, at Grand Teton (Climber's Ranch) almost every *D. tridentata* web contained seeds from neighboring cottonwood trees. Webs built on walls of buildings were even more prone to be covered by dust, sometimes causing these webs to be very conspicuous (fig. 3). Dry, hollow carcasses of insects, probably prey remains, were frequently found in the webs of virtually all species (JACKSON, 1978a). In the communal webs of *M. gregalis* in the laboratory, great numbers of fly carcasses accumulate (fig. 7), and there is no evidence that the spiders ever remove them. Instead, new silk seems to be simply added over the carcasses. Possibly in nature much of the debris from prey is removed by beetles that live with the spiders in the webs (DIGUET, 1909a, 1909b, 1915; GERTSCH, 1949).

NESTS

The nest (retreat) is an area of more densely woven silk within the mesh (fig. 1 and 4). Sometimes it was nearly opaque, but in other webs it was only slightly more dense than the mesh and not very conspicuous. Usually the shape was that of a hollow tube, with an opening at one or both ends, which is apparently the most common shape for spider nests (McCOOK, 1889; JACKSON, 1978b; for other shapes of dictynid nests, see NIELSEN, 1931). Generally individual webs and web units within web complexes each had a single nest. The spiders tended to occupy nests when not feeding, spinning or otherwise active. Sometimes the margins of the entrance to nests (doors) were reinforced, forming a "gate" (WIEHLE, 1953).

The sizes of nests were not recorded, and this would have been quite difficult in most cases because the boundaries of the nests were often not distinct. It was noted, however, that most were approximately 1 cm in length; but this tended to vary appreciably, ranging from not much larger than the spider to ones exceeding 3 cm in length (fig. 1).

In the case of *D. phylax*, when webs were found on conifer trees, the nests were nearly always (83%) fastened to the primary stem and the needles. In the case of the *Dictyna* sp. (San Anton Falls) that built webs on rolled leaves, the nest was always under one of the rolled edges of the leaf. Considering only those webs built on shrubs and herbs for the remaining solitary species, 18.29% had nests inside or under dead leaves. (See below for sample sizes for each species.) The leaves were dry, and usually they were rolled or folded over to varying degrees. Nests were under dead flowers in 17.07 % of the webs. In 48.78 % of the webs, the nest was at a fork in the primary stem (fig. 1); in 14.78%, beside the primary stem but not at a fork; and in the mesh but not next to a stem, leaf, or flower in one web.

In the case of *M. niveus* webs on walls of buildings, sometimes nests were constructed partially or entirely inside cracks between bricks or in other crevices (fig. 3). Nests of *M. trivittatus* and *D. calcarata* were frequently found partially inside crevices on bark of trees, rock ledges, walls of building, and so forth. Frequently nests were situated amongst moss (fig. 6) or lichen on rocks or trees. Also nests were generally under a mass of debris such as insect carcasses, regardless of whether they were also inside a crevice or under moss or lichen. Other authors have noted the tendency of dictynid nests to be situated in crevices or holes in the substrate.

Considering 85 vertically oriented individual webs (*M. niveus*, 33; *Mallos* sp., Lake Chapala, 2; *D. annexa*, 11; *D. coloradensis*, 6; *D. phylax*, 6; *D. tridentata*, 15; *D. tucsona*, 4; *Dictyna* sp., Querecho plains, 8) on herbaceous plants and shrubs, the nests of most were in the middle (54.12%) or upper (40.00 %) third of the web; and only 5.88 % were in the lower third.

It seems likely that nests function in protection from predators and parasitoids; and various hypothetical mechanisms of this, proposed for vagabond spiders in the family *Salticidae* (JACKSON, 1977b), would seem applicable to the dictynids also. The location of the nest within the web would seem to be an additional factor of importance for the dictynids. To reach the nest, the predator would have to cross a sizable portion of the mesh web, since nests were never at the periphery of the web. This probably delays the predators and provides the resident with early detection of the predator's approach. Placement of nests in concealed places, such as in crevices, beside a stem, and so forth, might be expected to increase the predators' problems in detecting the spider and capturing it once it has been detected.

	M. niveus	*Mallos* sp. (Lake Chapala)	*D. annulipes*	*D. completa*	*D. tridentata*	*Dictyna* sp. (Querecho Plains)
Number of webs per plant:						
Two, only one occupied	2	0	0	0	4	2
Two, both occupied	4	2	2	0	0	0
Three, only one occupied	0	0	0	0	0	1
Three, only two occupied	1	0	0	6	1	4
Four, only two occupied	0	0	0	1	0	2
Distances between webs on same plant:						
Both occupied	74 ± 45.1 (5)	10, 10	30, 30	69 ± 57.8 (7)	15	17 ± 14.4 (6)
One occupied, other one not occupied	53 ± 37.7 (4)	-	-	70 ± 38.4 (16)	27 ± 6.1 (6)	26 ± 17.0 (20)

Table 6 - Occurence of more than one web of the same species of solitary dictynid on single herbs and shrubs. Occupied: containing spider of indicated species. Unoccupied dictynid webs on same plant assumed to have been built by the indicated species. Distance: mean ± S.D. (number measured), measured within 5 cm of the most near edges. Actual measurements instead of means given when N = 2 or 1. Touching webs excluded. Plants with only one web or only unoccupied webs excluded.

SPACING OF INDIVIDUAL WEBS

In most cases of individual webs built on shrubs and herbs, there was only one dictynid web per plant. Exceptions occured in six species (table 6). The distance to the nearest neighboring web on the same plant was 44 ± 37.9 cm. There were no significant differences related to the species involved or whether the neighboring web was occupied or not (see table 6). Often more than one web of *D. phylax* was found on the same tree, but counting these was not practical. The only cases in which individual webs were found in conspicuous aggregations were some webs of *M. niveus* on the walls of buildings in Guanajaato (fig. 3), and the spacing of these is discussed elsewhere (JACKSON and SMITH, 1978).

CONNECTED INDIVIDUAL WEBS

When all solitary species are considered, 402 occupied webs were observed in nature. A spider was in a web that was connected by silk to another web occupied by a conspecific individual in only one instance. this was a pair of webs on a wall in Guanajaato, each occupied by an immature *M. niveus*. In another two cases, pairs of webs on walls in Guanajaato were connected to each other, but in each of these only one web was occupied. The only other observed case of connected webs of a solitary species was a female of *Dictyna* sp. (Querecho Plains), in a web with a few lines of silk connected to a similar unoccupied web on the same shrub. BILLAUDELLE (1957) noted that when the webs of *D. civica* become especially cluttered with debris and dust, the occupant may desert its web and build a new one connected to the old one. This is one possible explanation for some of the cases in this study of occupied webs connected to unoccupied ones.

ISOLATED WEBS OF COMMUNAL, TERRITORIAL SPECIES

Although these species were usually found in web complexes, occasionally (68 webs) they were found in isolated webs, defined as ones not connected by silk to other webs of conspecifics; i.e., they were not parts of web complexes. Most (56) occupied isolated webs were within 1 m of other occupied isolated webs or web complexes. The other 12 were found greater distances from other occupied webs, although occupied web complexes were in the general area in each case.

In 29 small web complexes only one occupied web unit was located. However, in some cases it was difficult to discount the possibility that some of the other web units were occupied, since nests tended to be located partially in crevices. Spiders possibly ran farther into the crevice before I noticed them.

At Chapala 25.47% of occupied webs on walls of buildings were isolated webs, but each was within 1 m of other webs occupied by conspecifics. At San Miguel de Allende 22 isolated webs containing *D. calcarata* were found on walls of buildings. Although no web complexes were found here, each web was within 1 m of other occupied webs.

Most of the *D. albopilosa* found at San Anton Falls were in web complexes. A few were in isolated webs, in close proximity of web complexes, and wrapped around the same type of vegetation. In nearby Cuernavaca 16 isolated webs containing *D. albopilosa* were found on walls of buildings, each web within 1 m of another occupied web.

Isolated webs of these species on walls of buildings, tree trunks, and other relatively flat surfaces resembled the individual webs of *M. niveus* on walls of buildings. However, isolated webs of *M. trivittatus*, like web units in web complexes, tended to have extension lines. Also, isolated webs of each communal, territorial species differed from individual webs of solitary species in that they were sometimes occupied by small groups of spiders of varying sex/age classes (JACKSON and SMITH, 1978).

Unlike the majority of webs of this species, four of the isolated webs of *M. trivittatus* were located on branches and stems of trees. One of these was constructed flat against the underside of a living limb (12 cm in diameter) of an oak tree, approximately 1.5 m above the ground. Three extension lines extended approximately 20 cm to a lower branch. Another web was on the underside of a 10 mm dead stem on an oak tree. This web was of particular interest because it had a latticework appearance, not so different from that of *M. niveus* webs, rather than being flat against the stem. Another two webs were found on dead stems (diameter of stems: 15 mm, 10 mm) of lodgepole pines: and these also had a latticework appearance, similar to the webs built by solitary species on stems. One web was 33 cm long and 7 cm wide. The other was 19 cm x 14 cm. One was 1 m and the other was 2 m above the ground. These three webs contrasted with the more common ones of this species in having much of the silk suspended away from, rather than flat against, the substrate. Also, several other webs on rocks and tree trunks, both isolated ones and web units complexes, were suspended to varying degrees. The manner in which this came about was that smaller diameter threads were strung in a widely spaced manner between several heavy extension lines, creating a web with a latticework appearance (fig. 6).

GROUP SIZE IN M. GREGALIS

Although study of natural populations in Mexico will be needed in order to determine the extent of variability in *M. gregalis*, some observations from the laboratory are of interest. The spiders were not confined, but allowed to colonize new web sites in the laboratory. Most spiders were in large communal webs with many other individuals. However, small communal webs containing only a few individuals were frequently found; and occasionally webs containing single individuals were seen. Also, individual females and immatures experimentally isolated from communal webs and maintened individually in plastic cages survived indefinitely on a diet of houseflies and/or *Drosophila*.

GROUPS OF SPIDERS SHARING INDIVIDUAL WEBS

There were two special circumstances in which a group of spiders of a solitary species were found sharing the same web: recently hatched immatures in webs with females and joint occupation of webs by male-female pairs. The pair could consist of an adult male with either an adult or large subadult female. The subadults were most likely ones that would mature at their next molt (JACKSON, 1978c).

Females of *M. niveus*, *D. tridentata*, and *Dictyna* sp. (Querecho Plains) were found with eggs in their webs. Usually eggs were situated in and around the nests, and often the female was inside the nest with her eggs. As many as three egg sacs were found side-by-side in the same web. *Dictyna* sp. (Querecho Plains) was the only species in with females were found with their recently hatched progeny. In some cases there were tiny spiderlings clustered around the egg sacs in webs containing females, and sometimes the female was surrounded as well. In other cases, tiny spiderlings, apparently first instar (terminology: WHITCOMB, 1973), were found scattered throughout the web.

SYMPATRY AMONG DICTYNID SPECIES

Many of the species in this study were sympatric with each other (table 7). Since I stayed only 2 or 3 hr in some habitats (table 1) these observations are only a minimal estimate of the amount of sympatry that occurs. Strict correlations between social organisation, habitats, and web sites did not occur.

HABITAT	SYMPATRIC SPECIES
Chiracahua Mountains	
Cave Creek Canyon	*Mallos niveus*, *Mallos trivittatus*, *Dictyna* sp.
East Turkey Creek	*Mallos niveus*, *Mallos trivittatus*
Rustler's Park	*Mallos trivittatus*, *Dictyna peon*
Grand Teton National Park, Leigh Lake	*Dictyna phylax*, *Dictyna tridentata*
Rocky Mountain	
Big Thompson Canyon	*Mallos niveus*, *Mallos trivittatus*, *Dictyna bellans*
Eastes Park	*Mallos trivittatus*, *Dictyna tridentata*
Wind River Range, Ring Lake	*Dictyna annulipes*, *Dictyna coloradensis*
San Anton Falls	*Dictyna albopilosa*, *Mallos dugesi*, *Dictyna* sp.

Table 7 - Sympatry of Dictynid species.

The communal and territorial species *M. trivittatus* was sympatric with several solitary species. In each case the species were sometimes found within less than 1 m of each other. For example, once at East Turkey Creek a *M. trivittatus* was found in an isolated web on an exposed root of a large shrub (*Fraxinus valentia*) with a *M. niveus* in a web less than 1 m away on a stem of the same plant; and the large web complex in the culvert was only a few metters away. Although *M. trivittatus* generally adopted relatively flat surfaces as web sites and the sympatric solitary species generally were found on stems of plants, web site separation by these species was not absolute (table 3).

The three sympatric species at San Anton Falls were each found within 1 m of each of the others. The *Dictyna* sp. that built webs on partially folded leaves was on a different type of vegetation from the other two species. However, *M. dugesi* and *D. albopilosa* shared the same plants, and sometimes the two species had lines of silk connecting their webs. This was the closest physical association between the two dictynid species found in this study.

The *Dictyna* sp. at Cave Creek Canyon was found on the same type of herbaceous plants as *M. niveus* and in one case within 2 m of a web occupied by *M. niveus*. The three species at Big Thompson Creek were each found within the same few square meters. At Leigh Lake *D. tridentata* and *D. phylax* did not overlap in web sites since the former were on shrubs and the latter were on trees. *D. tridentata* were in small clearings, several meters from the nearest *D. phylax* in the surrounding forest. However, in other habitats, a few *D. phylax* were found on herbs and shrubs (table 3), indicating that web site specificity was not absolute. *D. annulipes* and *D. coloradensis* were found on the same types of plants, sometimes within 1 m of each other at Ring Lake, but never on the same individual plant.

These observations raise the question of how sympatric dictynid species avoid competitive exclusion. Although web site specificity may play a role in some cases, the great intraspecific variability found for some species cautions against hasty conclusions. Future long-term studies should investigate other factors such as phenology and prey selection; but most importantly, studies are needed to clarify the degree of competition that occurs between coexisting species (see WIENS, 1977).

LONGEVITY OF WEBS

We do not have data concerning exactly how long webs are used by dictynids in nature, but dictynid webs seem to be relatively permanent structures compared to the orb webs of araneids, for example (see WITT, REED, and PEAKALL, 1968). The possible selection of dead stems as web sites by *Dictyna* and *Mallos* species may be related to the relatively long endurance of their webs. Perhaps a growing, green stem is a less suitable web site because it requires rather much maintenance concurrent with growth of the plant. Also, a web on a green stem may suffer from greater risks of inadvertent destruction or damage by feeding herbivores.

Web complexes may have greater longevity than individual webs. In some web complexes of each species, the mesh web was quite dense, completely concealing the substrate beneath; but webs of solitary species were generally less dense. In many cases the term "sheet web" is more appropriate for web units than "mesh web". Since the web complex in the culvert at East Turkey Creek had been seen by other people several years earlier (V.D. ROTH, personal communication), it seems likely that web units in some web complexes are used by successive generations of spiders and that new silk is continually added, gradually incrasing the density of silk in the web. It is noteworthy in this connection that juvenile *D. civica*, a species that occurs in aggregations of individual webs on walls of buildings, will use abandoned webs of adult for at least a few weeks after hatching (BILLAUDELLE, 1957).

In the laboratory, populations of *M. gregalis* have lived in the same communal webs for several years, to which they continually add fresh silk. Although DIGUET (1909a) made reference to *M. gregalis* adults abandoning their communal webs at the end of the rainy season, so few field observations have been carried out with this species that its life history in Mexico is quite unclear at this time.

GENERAL DISCUSSION

The distinction between a web complex and an individual web seems not so enormous. If we assume that the species which build web complexes evolved from species that built individual webs, the most important steps would seem to be a tendency to place webs in close proximity and a certain degree of tolerance for conspecific individuals in touching webs. If we assume that *M. gregalis* evolved from a species that constructed web complexes, perhaps similar to those of *D. albopilosa* on vegetation, the necessary steps would seem to be incrassed tolerance of conspecific individuals in close proximity and elimination of tendencies to confine spinning behavior within a single web unit. The result would be a large sheet web, with neither boundaries nor interstitial web areas, perhaps not so different from a *M. gregalis* communal web. More information concerning the manner in which each type of dictynid constructs its webs would be very valuable.

Since social organisation was found to vary widely within a single group of closely related species, the results of this study are consistent with the hypothesis that social organisation is among the most evolutionarily labile traits of animal species (WILSON, 1975). Similar wide variation within groups of related species occurs in other spider families (e.g., see KRAFFT, 1970).

Generally spiders live in an aggregation for a period after hatching. The duration of this period varies from species to species, but the duration of the postembryo stage and at least part of the first instar seems to be most common. The potential significance of this phenomenon in the evolution of social spiders has been considered by BERLAND (1928), KRAFFT (1970), and KULLMANN (1968, 1972, 1975). The tendency of the early instars to aggregate may have been a behavioral substrate on which natural selection has acted during the evolution of spider sociality. In some species, the spiderlings remain together with the mother for several instars; maternal care, including feeding of the spiderlings by regurgitation, may occur; and the spiders disperse before maturing. KULLMANN (1968, 1972) referred to these as "periodic-social" species, and he suggested that "permanent social" species, in which the adults remain together, evolved by extending this trend into adult life.

One of the important future tasks will be to determine how appropriate this hypothesis is for the dictynids. Spiderlings of only one solitary species have been observed in this study; and there was no evidence of prolonged aggregation since all were apparently first instar spiderlings. Since BRISTOWE (1958) noted that immatures of some solitary dictynids remain in the maternal web for prolonged periods, further investigation of this question would be valuable. BRISTOWE reported that the spiderlings fed on insects in the web; however, regurgitation-feeding has not been reported in dictynids.

Since web units of the communal and territorial species generally contained either one spider or a small group consisting of individuals of varying sex/age classes, it seems unlikely that siblings of single broods remain together for prolonged periods, in the same web unit, although they may remain in the same web complex. Hypothetically, some spiderlings eventually build new web units within the web complex of origin; others disperse away from the web complex; and still others enter existing web units in which they are tolerated if they do not overlap in size with resident spiders.

More information concerning the Australian dictynids in the genus *Ixeuticus* would be valuable for comparison with *Dictyna* and *Mallos*. Some species live in individual webs. From MAIN's (1971) brief descriptions, it seems that juveniles of *I. candidus* build web complexes on vegetation around the mother's web; but they disperse and live in individual webs when mature. Other species live on vegetation and in caves (McKEOWN, 1963) in webs that may resemble the communal webs of *M. gregalis*.

The family *Amaurobiidae* is closely related to the *Dictynidae*, and at times the two families have been treated as a single family. It is noteworthy that webs of some Australian Amaurobiids may be similar to the communal webs of *M. gregalis* (BERLAND, 1932; GERTSCH, 1949; RAINBOW, 1905).

It has frequently been argued that the adaptative significance of territorial behaviour in animals is related to the territorial individual gaining exclusive or nearly exclusive access to a set of resources within the defended area (see BROWN, 1975; WILSON, 1975). A web unit within a web complex might contain a number of resources the defense of which would be optimal for the resident spiders. The mesh and especially the nest might be an important resource related to protection from predators. Also, males may treat females within web units as resources that they defend against other males. However, the most important factor may be that the mesh is a prey capturing device. The web unit can be viewed as a food resource containing the prey made available by means of the mesh.

A question on which future ecological studies should focus concerns the factors which favor territorial behavior in one set of communal species and sharing of the web and prey in another species, *M. gregalis*.

We can now return to the question raised at the beginning of this paper: what are the characteristics of "social spiders"? A useful approach to this question is the set of three criteria proposed by KULLMANN (1968, 1972): tolerance, interattraction, and cooperation. Tolerance refers to the fact that social spiders are not very cannibalistic or aggressive toward each other. Interattraction (DARCHEN, 1965) refers to the fact that social spiders occur in groups because they are attracted to each other in some sense, rather than because they are attracted in common to some factor in the environment. Although cooperation is a difficult concept to define, it may be the most important criterium. As WILSON (1975) pointed out, this concept repeatedly turns up either explicitly or implicitly in definitions of sociability; and it seems to be close to the essence of what is interesting about animals that we think of as social. The intuitive idea is that the cooperative individual does things that are somehow for the benefit of other individuals in the society (WILSON, 1975). Also a certain degree of coordination of activities would seem to be part of the concept (SUDD, 1963). Comparative studies in this laboratory are presently investigating dictynid spiders with respect to KULLMANN's three criteria.

If one had to choose a single characteristic of spiders that is most important for understanding adaptation and diversity in this group, it would probably be silk production. Spiders are perhaps largely the product of an evolutionary lineage entering an adaptative zone (SIMPSON, 1953) that is somehow defined by the use of silk. Vagabond spiders use silk for construction of nests, enclosure of eggs, sperm induction, courtship, etc. When it comes to web-building spiders, any reasonably complete understanding of these species would seem to demand a thorough knowledge of their silk-related behavior and the characteristics of their webs. In the present work with dictynids, web characteristics have proven integral to understanding social organization. Three basic types of social organization occur, with three corresponding types of webs.

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REFERENCES

BEER, C.G., 1977 - What is a display? — *Amer. Zool.*, **17** : 155 - 165.

BERLAND, J., 1916 - Note préliminaire sur le cribellum et le calamistrum des Araignées cribellates et sur les moeurs de ces Araignées. — *Arch. Zool. expér. gén.*, **55** : 53 - 66.

BERLAND, L., 1913 - Utilisation pour la capture des Mouches, des nids de l'Araignée mexicaine Coenothele gregalis E. Simon. — *Bull. Mus. hist. nat.*, **1913** : 432 - 433.

BERLAND, L., 1928 - La répartition géographique des Araignées sociales. — *C.R. Soc. biogéogr.*, **37** : 33 - 36.

BILLAUDELLE, H., 1957 - Zur Biologie des Mauerspinne Dictyna civica (H. Luc.)(Dictynidae, Araneida). — *Z. Angew. Entomol.*, **41** : 475 - 512.

BLANKE, R., 1972 - Untersuchungen zur Ökophysiologie und Ökethologie von Cyrtophora citricola Forskal (Araneae, Araneidae) in Andalusien. — *Forma et Functio*, **5** : 125 - 206.

BRACH, V., 1975 - The biology of the social spider Anelosimus eximus (Araneae: Theridiidae). — *Bull. S. California Acad. Sci.*, **74** : 37 - 41.

BRACH, V., 1977 - Anelosimus studiosus (Araneae: Theridiidae) and the evolution of quasisociality in theridiid spiders. — *Evolution*, **31**: 154 - 161.

BRISTOWE, W.S., 1941 - The comity of spiders, vol. II. — *Ray Society, London.*

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

BROWN, J.L., 1975 - The evolution of behavior. — *Norton, New York.*

BURGESS, J.W., 1976 - Social spiders. — *Sci. Amer.*, **234** : 100 - 106.

BURGESS, J.W., 1978 - Social behavior in group-living spider species. — *Symp. Zool. Soc. London*, in press.

BURGESS, J.W. & WITT, P.N., 1976 - Spider webs: design and engineering. — *Interdispl. Sci. Rev.*, **1** : 322 - 335.

BUSKIRK, R.E., 1975 - Aggressive display and orb defense in a colonial spider, Metabus gravidus. — *Anim. Behav.*, **23** : 560 - 567.

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

CHAUVIN, R. & DENIS, J., 1964 - Une nouvelle espèce d'Araignée sociale, Agelena consociata Denis. — *Biol. Gabonica*, **1** : 93 - 99.

CLYNE, D., 1969 - A guide to Australian spiders. — *Nelson, Melbourne.*

COMSTOCK, J.H., 1912 - The spider book. — *Doubleday, New York.*

DARCHEN, R., 1965 - Ethologie d'une araignée sociale, Agelena consociata Denis. — *Biol. Gabonica*, **2** : 117 - 146.

DARCHEN, R., 1968 - Ethologie d'Achaearanea disparata Denis, Araneae, Theridiidae, araignée sociale du Gabon. — *Biol. Gabonica*, **4**: 5-25.

DARCHEN, R., 1973 - L'Ecologie d'une araignée sociale (Agelena consociata D.) à la lumière de quelques expériences de laboratoire. —*Insectes Sociaux*, 20 : 379 - 384.

DARCHEN, R., 1975 - Les communications sociales chez Agelena consociata D. (Aranéide, Labidognathe). — *C.R. Acad. Sci., Paris*, 281 : 575-578.

DARCHEN, R., 1977 - La fondation de nouvelles colonies d'Agelena consociata et d'Agelena republicana, araignées sociales du Gabon. Problèmes éco-éthologiques. Pp. 20-39, *in*: Troisième réunion des arachnologistes d'expression française (= C. R. Col. Arachnologie Fr.), Les Eyzies, 1976.

DIGUET, L., 1909a - Sur l'araignée mosquero. — *C. R. Acad. Sci., Paris*, 148 : 735 - 736.

DIGUET, L., 1909b - Le mosquero. Nid d'Araignée employé dans certaines régions du Mexique comme piège à mouches. — *Bull. Soc. Acclim. France*, 56 : 368 - 375.

DIGUET, L., 1915 - Nouvelles observations sur le mosquero ou nid d'Araignées sociales employé comme piège à mouches dans certaines localités du Mexique. — *Bull. Soc. Acclim. France*, 62 : 240 - 249.

FORSTER, R.R. & FORSTER, L.M., 1973 - New Zealand spiders. — *Collins, Auckland.*

GERTSCH, W.J., 1949 - American spiders. — *Van Nostrand, Princeton.*

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 - Predation as a selection factor in the mating strategy of the jumping spider Phidippus johnsoni (Salticidae, Araneae). — *Psyche*, 83 : 243 - 255.

JACKSON, R.R., 1978a - Comparative studies of Dictyna and Mallos (Araneae, Dictynidae): III. Prey and feeding behavior. — In prep.

JACKSON, R.R., 1978b - Nests of Phidippus johnsoni (Araneae, Salticidae): characteristics, pattern of occupation and function. — In Review.

JACKSON, R.R., 1978c - Web sharing by males and females of dictynid spiders. — *Bull. Brit. Arachn. Soc.*, in press.

JACKSON, R.R. & SMITH, S.E., 1978 - Aggregations of Mallos and Dictyna (Araneae, Dictynidae): population characteristics. — In prep.

KASTON, B.J., 1948 - Spiders of Connecticut. — *Bull. Connecticut Geol. Nat. Hist. Survey*, 70 : 1 - 874.

KRAFFT, B., 1969 - Various aspects of the biology of Agelena consociata Denis when bred in the laboratory. — *Amer. Zool.*, 9 : 201 - 210.

KRAFFT, B., 1970a - Contribution à la biologie et à l'éthologie d'Agelena consociata Denis (Araignée sociale du Gabon). Première partie. — *Biol. Gabonica*, 6 : 197 - 301.

KRAFFT, B., 1970b - Contribution à la biologie et à l'éthologie d'Agelena consociata Denis (Araignée sociale du Gabon). Deuxième partie. — *Biol. Gabonica*, 6 : 307 - 369.

KRAFFT, B., 1971 - Contribution à la biologie et à l'éthologie d'Agelena consociata Denis (Araignée sociale du Gabon). Troisième partie. Etude expérimentale de certains phénomènes sociaux. — *Biol. Gabonica*, 7 : 3 - 56.

KRAFFT, B., 1975 - La tolérance réciproque chez l'araignée sociale Agelena consociata Denis. — *Proc. 6th Internat. Arach. Congr.*, 1974 : 107-112.

KULLMANN, E., 1968 - Soziale Phaenomene bei Spinnen. — *Insectes Sociaux*, 15 : 289 - 297.

KULLMANN, E., 1969 - Beobachtungen zum Sozialverhalten von Stegodyphus sarasinorum Karsch (Araneae, Eresidae). — *Bull. Mus. Nat. Hist.*, (1) 41, suppl. 1 : 76 - 81.

KULLMANN, E., 1972 - Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). — *Amer. Zool.*, 12 : 419 - 426.

KULLMANN, E., NAWABI, S. & ZIMMERMANN, W., 1972 - Neue Ergebnisse zur Brutbiologie cribellater Spinnen aus Afghanistan und der Serengeti (Araneae, Eresidae). — *Z. Kölner Zoo*, 14 : 87 - 108.

KULLMANN, E. & ZIMMERMANN, W., 1975 - Regurgitationsfütterungen als Destandteil der Brutfürsorge bei Haubennetz und Röhrenspinnen (Araneae, Theridiidae und Eresidae). — *Proc. 6 th Internat. Arach. Congr.*, 1974 : 120 - 124.

LEHTINEN, P.T., 1967 - Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. — *Ann. Zool. Fenn.*, 4 : 199 - 468.

LOCKET, G.H. & MILLIDGE, A.F., 1951 - British spiders, vol. 1. — *Ray Society, London.*

LUBIN, Y.D., 1974 - Adaptative advantages and the evolution of colony formation in Cyrtophora (Araneae: Araneidae). — *Zool. J. Linn. Soc.*, 54 : 321 - 339.

MAIN, B.Y., 1971 - The common "colonial" spider Ixeuticus candidus (Koch) and its synonyms (Dictynidae: Araneae). — *J. Roy. Soc. W. Australia*, 54 : 119 - 120.

MASCORD, R., 1970 - Australian spiders in coulour. — *Tuttle, Rutland, Vermont.*

McCOOK, H., 1889 - American spiders and their spinningwork, vol. I. — *Philadelphia.*

McKEOWN, K.C., 1936 - Spider wonders of Australia. — *Angus & Robertson, Sydney.*

NIELSEN, R., 1931 - The biology of spiders, vol. I. — *Levin and Munskgaard, Copenhagen.*

PAIN, G., 1964 - Premières observations sur une espèce nouvelle d'Araignées sociales, Agelena consociata Denis. — *Biol. Gabonica*, 1 : 47 - 58.

PEAKALL, D.B., 1968 - The spider's dilemma. — *New Scientist*, 4 : 28 - 29.

RAINBOW, W.J., 1905 - Studies in Australian Araneidea. No 4. — *Rec. Austral. Mus.*, 6 : 9 - 12.

SEMICHON, L., 1910 - Observations sur une araignée mexicaine transportée en France. — *Bull. Soc. Entomol. France*, 1910 : 338 - 340.

SIMON, E., 1909 - Sur l'Araignée mosquero. — *C. R. Acad. Sci., Paris*, **148** : 736 - 737.

SIMPSON, G.G., 1953 - The major features of evolution. — *Columbia university Press, New York.*

SUDD, J., 1963 - How insects work in groups. — *Discovery* : 15 - 19.

WHITCOMB, W.H., 1978 - Ontogeny of North American wolf spiders. — *Symp. Zool. Soc. London,* in press.

WIEHLE, H., 1953 - Spinnentiere oder Arachnoidea (Araneae). IX: Orthognatha, Cribellatae, Haplogynae, Entelegynae (Pholcidae, Zodariidae, Oxyopidae, Mimetidae, Nesticidae). *in* : DAHL, F. (ed.) Die Tierwelt Deutschlands. — *Fischer, Iena.*

WIENS, J.A., 1977 - On competition and variable environments. — *Amer. Sci.*, **65** : 590 - 597.

WILSON, E.O., 1971 - The insect societies. — *Belknap, Cambridge, Massachusetts.*

WILSON, E.O., 1975 - Sociobiology. — *Belknap, Cambridge, Massachusetts.*

WITT, P.N., REED, C.F. & PEAKALL, D.B., 1968 - A spider's web. — *Springer Verlag, New York.*