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ORB-WEAVING SPIDERS IN AGGREGATIONS MODIFY INDIVIDUAL WEB STRUCTURE[1]

Ruth E. Buskirk

Institute for Geophysics and Brackenridge Field Laboratory
University of Texas at Austin
Austin, Texas 78713

ABSTRACT

Orb-weaving spiders that live in groups modify their web structure and activity periods, in contrast to solitary araneids that build more individually distinctive orbs. Individually marked spiders (n = 62) of the colonial *Metabus gravidus* (Araneidae) in Costa Rica were monitored for 5-day periods during which all webs spun were measured. Variation in web characters (particularly web angle and viscid spiral measures) within an individual is related to time of day and degree of aggregation. Comparisons of six orb-weaving species suggest that spiders joining aggregation vary their web characteristics when in groups.

INTRODUCTION

The geometric orb webs of spiders in the families Araneidae, Uloboridae, and Tetragnathidae usually have characteristics that are typical of the genus or species (Risch 1977, Eberhard 1982). In addition, individual spiders that build their orbs in a controlled environment, with standarized web support structures and attachment sites, often build orbs of the same size and pattern day after day (Witt et al. 1968, Peters 1969). Changes in web structure with age of spider, molting condition, nutritional status, configuration of attachment sites and time of day have all been documented especially in laboratory work (Szlep 1958, 1961, Witt et al. 1968, Peters 1970, Eberhard 1972, Ramousse and LeGuelte 1984). Variability of web structure under natural conditions has not been as well quantified.

Previous observations of the colonial spider *Metabus gravidus* (Cambridge) (Araneae, Araneidae) in Costa Rica (Buskirk 1975a) suggested that orb structure was highly variable within an individual, unlike the comparatively predictable orbs found in laboratory studies of other araneids (e.g., Witt et al. 1968). For this study I gathered data on webs of these colonial spiders, both those in aggregations and a few isolated individuals, to determine the effect of colony participation on orb structure. For additional comparison I analyzed webs of other orb-weaving species which occasionally formed aggregations. This study determines the extent of individual variation in orb webs in different species and its relation to the tendency of the species to form aggregations.

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METHODS

The colonial orb-weaving spider *M. gravidus* is abundant at the study site chosen on the Rio Guacimal (Monteverde, Costa Rica, elevation 1350 m). Individually marked adult or subadult females were monitored hourly for periods of 5 days in June or July (rainy season), during which every orb spun was measured. Each of 62 individuals built at least 5 orbs, and some as many as 14 orbs, during the observation periods. About 15% of these orbs were webs rebuilt in the same site. In this process the old web is destroyed, and the spider immediately reinforces support lines and radii then completely renews the viscid spiral. In all webs I measured radius, number of radii, number of spiral turns, and angle from the horizontal.

RESULTS FOR A COLONIAL SPECIES

Orb web measurements of individual *M. gravidus* in colonies can vary more than 30% within a period of a day or two. For example, the web formula consisting of (A) number of radii, (B) number of spiral turns and (C) orb radius in cm varied as follows for one adult female (day and time, A, B and C, respectively): day 1 (07:00 h)—13, 18, 15.0; day 1 (17:30 h)—11, 15, 12.8; day 2 (12:00 h)—12, 11, 12.2; day 3 (06:30 h)—9, 16, 10.8; day 3 (17:00 h)—10, 17, 14.0. In a sample of webs the variability within individuals was as great as between individuals for the orb radius and number of radii, as shown below.

One source of high variance in orb measures in *M. gravidus* is the time of day at which orbs are built. These spiders may emerge from the retreat and build a new orb at any daylight hour (Buskirk 1975a) and often respin webs once or twice during the day. Webs either built or respun in the last two hours of the diurnal activity period (Evening Webs in Table 1) have significantly smaller radii ($t = 2.39$, $p < 0.025$), fewer radii ($t = 2.70$, $p < 0.01$) and larger mesh size ($t = 2.81$, $p < 0.01$) than morning webs. Analysis of variance for radius length and number of radii, however, indicates that even when morning and evening webs are distinguished, variability within a spider is high (Table 1).

In 169 web-spinning observations spiders averaged a speed of nearly one cm/sec in spinning the viscid spiral, but there was much variation over the day. At dawn (06:00-07:00 h) the sticky thread of the viscid spiral was spun at a quicker rate than in mid-morning ($t = 2.41$, $p < 0.05$) with no significant changes in radius or mesh. In the evening period (16:00-18:00 h) an increased speed (1.4 cm/sec) is accompanied by a smaller average radius (9.7 cm) and coarser mesh (6.1 sq. cm). These times of rapid spinning (dawn and dusk) coincide with heightened insect activity, and the evening period is one of increased number of adult spiders occupying and building orbs (Buskirk 1975a).

To test the effect of the colony participation on orb variance, I examined web radius and number of radii in all webs spun by 62 individually marked spiders during the five day observation period. Ten spiders that were temporarily isolated and not building in colonies built less variable webs than the other 52 individuals that built in colonies. For example, variance of the radius length (mean = 13.2 cm) in all orbs spun by a given individual ranged from 0.6-6.7 in aggregated individuals but was only 0.8-3.0 in solitary spiders. Orb radius varied at least 50%

Table 1.—Individual variability of orb webs in 62 *Metabus gravidus* adult female spiders within a colony (p values are for One-Way ANOVA; ** indicates $p < 0.10$; NS indicates $p > 0.10$.) For time of day analysis time blocks used were 06:00-09:00 h (morning webs), 10:00-12:00 h, 13:00-15:00 h, and 16:00-17:00 h (evening webs).

		Morning Webs Combined:	Evening Webs Combined:
Radius	$\bar{x} \pm$ s.d.	13.2 ± 4.0 cm	11.7 ± 3.7 cm
	ANOVA, by spider	** ($p < 0.05$, df 5, 14)	** ($p < 0.02$, df 5, 14)
	ANOVA, by date	NS ($p > 0.10$, df 5, 14)	NS ($p > 0.10$, df 5, 14)
	ANOVA, by time	All Webs:	** ($p < 0.02$, df 3, 40)
Number of Radii:	$\bar{x} \pm$ s.d.	11.5 ± 4.2	8.2 ± 5.3
	ANOVA, by spider	** ($p < 0.05$, df 5, 14)	** ($p < 0.05$, df 5, 14)
	ANOVA, by date	** ($p < 0.05$, df 5, 14)	** ($p < 0.05$, df 5, 14)
	ANOVA, by time	All Webs: **	($p < 0.10$, df 3, 40)
Mesh:	$\bar{x} \pm$ s.d.	3.9 ± 2.1 cm^2	5.8 ± 3.9 cm^2
	ANOVA, by spider	NS ($p > 0.10$, df 5, 14)	NS ($p > 0.10$, df 5, 14)
	ANOVA, by date	NS ($p > 0.10$, df 5, 14)	NS ($p > 0.10$, df 5, 14)
	ANOVA, by time	All Webs:	NS ($p > 0.10$, df 3, 40)

of the mean radius for over a third of the clustered individuals. Previous measurements (Buskirk 1975a) indicate that the average orb radius in the direction of a close neighbor (within 25 cm) was shorter than other radii of the same orb, presumably as a result of aggressive encounters with the neighbor during orb construction (Buskirk 1975b).

EFFECTS OF CLUSTERING IN OTHER ORB-WEAVING SPIDERS

In other species of facultatively gregarious spiders, joining an aggregation may also have an effect on web-building. I observed six other species of orb-weavers at field sites in Texas and Costa Rica (see Table 2). The species examined represent spectrum of gregarious tendencies from those like *M. gravidus* in which spiders routinely cluster their orbs to those species which rarely cluster. Web characters chosen for comparison were orb radius, angle of the orb's plane from horizontal and presence of any unique structural elements such as barrier webs. I determined the percent of individuals aggregated from censuses of 30 or 50 individuals of each species. Additional spiders were surveyed for web measures. Web data (radius and angle) from aggregated individuals were considered different from those of solitary individuals if they were significant at the $p < 0.05$ level (Mann-Whitney U test).

As indicated in Table 2 some web characters varied with degree of aggregation. In Texas webs of *Nephila clavipes* (Linnaeus) and *Mecynogea lemniscata* (Walckenaer) are occasionally found in clusters, especially in open woodland or edge areas where insects are abundant and web support structures are not limited. Aggregated females of these species use the support lines of their neighbors as web attachment points, but they do not generally modify their web by reducing the knockdown strands or barrier webs. Presence of barrier webs in *N. clavipes* may vary, but no consistent pattern in aggregations has yet been determined (L. Higgins, pers. comm.). Similarly, *Metazygia wittfeldae* (McCook), which are usually solitary, do not produce smaller or modified webs when they aggregate,

Table 2.—Web characteristics in seven orb weaving species that aggregate occasionally (top of list) or regularly (bottom of list). Yes = web radius or angle from horizontal was significantly different in clumped individuals (Mann-Whitney U test, $p < 0.05$). *= in one case barrier web was reduced.

Species and Site	Number Censused	Percent Sharing Support Lines	Smaller Orbs in Clusters?	Different Web Angle in Clusters?	Orb Structure Modified in Clusters?
Metazygia wittfeldae (Monteverde, Costa Rica)	50	6%	No	No	No
Mecynogea lemniscata (Austin, Texas)	30	7%	No	No	No
Nephila clavipes (Galveston, Texas)	50	10%	No	No	No*
Tetragnatha elongata (Austin, Texas)	50	20%	Yes	No	No
Leucauge venusta (Monteverde, Costa Rica)	50	34%	No	Yes	No*
Cyclosa caroli (Monteverde, Costa Rica)	50	52%	Yes	Yes	Yes
Metabus gravidus (Monteverde, Costa Rica)	50	90%	Yes	Yes	No

and the angle of the web continues to vary from just above horizontal to vertical (Table 2).

Like *M. gravidus* , *Tetragnatha elongata* (Walckenaer) build simple wide-meshed orbs, often over water. In tetragnathid aggregations I found orb radii to be shorter, but no other structural modifications were noted. Solitary *T. elongata* adults prefer to build horizontal orbs, but in aggregations the angle of the web differed from horizontal. When adult females of *Leucauge venusta* (Walckenaer) build in aggregations, they put their orbs in a more nearly horizontal plane and spin less dense support threads than do solitary individuals. Despite the presence of such modifications, the orb radius in these aggregated *L. venusta* webs did not differ significantly from that of solitary webs. On the other hand, aggregated individuals of *Cyclosa caroli* (Hentz) displayed a typical vertical web but produced smaller orbs.

VARIABILITY IN ORB-BUILDING

Several factors are known to contribute to the dimensions and regularity of web structures. Reed et al. (1965) and Eberhard (1972) found spiders can regulate orb structure and central angles via measuring behavior of the first pair of legs. During ontogeny, web mesh size increased in *Araneus diadematus* (Clerck) (Witt and Baum 1960). Mesh width is directly correlated with leg length, especially in adults (Risch 1977). Benforado and Kistler (1973) found that web radius increases with body size within an age class, primarily as a result of differential feeding. In comparison to individuals whose webs are destroyed, spiders permitted to ingest their web daily produce subsequent orbs up to 15% larger in radius with the number of spiral turns greater by 17-38% (Witt et al. 1968).

Species-specific patterns of orb-building and placement of radii account for some differences in variability. For example, Nentwig (1983) found that the mesh size and distance between spirals were much more variable in *A. diadematus* than in species such as *Zygiella x-notata* (Clerck) which insert additional radius lines midway out from the hub. Web-building traits such as hub construction, spiral attachment, and placement of barrier webs are typical of the genus (Eberhard 1982). In species that normally add barrier webs near the orb, individuals joining aggregations can construct webs with reduced or no barrier webs. Since barriers are usually constructed later than the frame and initial orb, sometimes hours or days later, the spider could receive feedback from the behavior of neighbors or prey capture rate that prevents barrier construction.

Orb size can depend upon the size of available area in the substrate for frame attachment. Adult *A. diadematus* in laboratory frames produced daily webs that varied in radius by less than 5% (Witt et al. 1968). The number of radii (means + s.d. = 26.1 + 4.2) and number of spiral turns (21.4 + 8.2) were more variable. Web radius and shape are modified, however, by *A. diadematus* as frame size decreases, while the angle of the web is last to change (Szlep 1958). In a field study of adult *Argiope trifasciata* (Forskal) and *A. aurantia* (Lucas), Brown (1981) found some variance in web radius, but variation was much greater for other measures such as web height. Studies of adult individuals of solitary orb-weavers show relatively little variance in web radius under standarized conditions.

SIGNIFICANCE FOR SPIDER SOCIAL BEHAVIOR

Two general evolutionary pathways to sociality in spiders have been proposed, one emphasizing prolonged parental care and cooperation within a cohort of young and one depending upon tolerance and aggregation of unrelated individuals (Shear 1970). Because orb-weavers must build orbs individually the degree of cooperation in producing a communal web is limited (Buskirk 1981). One might predict that stereotyped, individual web-building would be more efficient and would confer a selective advantage to orb-weaving spiders in general.

On the other hand, there are ecological advantages for building webs in aggregations. Field observations and manipulations of social and facultatively social spiders have confirmed that spiders are more likely to aggregate in rich prey patches and obtain as much or more food per individual in these groups (Buskirk 1975a, Uetz et al. 1982, Rypstra 1983, 1985, Riechert 1985). The tendency to cluster is strongest when food and web attachment sites are patchy. Long-term aggregation may also provide protection from predators or climatic changes. In addition, web clustering may result in more silk lines per individual for entangling and slowing down prey (Burgess 1978).

In aggregations the higher density of spiders will be costly if there is much effort spent in defending individual areas and if many supplantings of individuals from their webs occurs. If species recognition and tolerance has evolved in the behavioral repertoire or if high prey capture rates induce tolerance (e.g., Rypstra 1983), then individual spiders can successfully occupy the aggregated webs for long periods of prey capture.

Besides the orb-weavers addressed in this study, other araneids show some modification of individual web structure when aggregated in favorable resource sites. *Metepeira spinipes* (Cambridge) build orbs in aggregations of up to hundreds of individuals, and group size is larger in areas of greater prey availability (Uetz et al. 1982). Larger colonies are more dense, with smaller individual web areas, and individuals share space web and support threads (Uetz and Burgess 1979). The congeneric *Metepeira datona* (Chamberlin and Ivie) in the Bahama Islands sometimes form aggregations and may share retreats (Schoener and Toft 1983). Web-sharing usually involves spiderlings or males associating with large females, not aggregations of adult females. Solitary webs of large spiders tend to be vertical and oriented to minimize the wind, while those in aggregations are more variable in position.

Spiders that join aggregations can modify their web-building behavior to increase both silk efficiency and tolerance of neighbors. In the groups surveyed in Table 2 species that are regularly found in clusters show more modification of orb structure. Patchy resources account for the ecological advantages of group living in these spiders. Behavioral adaptability, in the form of variability in web construction, allows these species to take advantage of the ecological opportunities. Species with greater ability to modify individual foraging strategies are more likely to be facultatively gregarious.

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LITERATURE CITED

Benforado, B. J. and K. H. Kistler. 1973. Growth of the orb weaver, *Araneus diadematus,* and correlation with web measurements. Psyche, 80:90-100.

Brown, K. M. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. Oecologia, 50:380-385.

Burgess, J. W. 1978. Social behavior in group-living spider species. Symp. zool. Soc. London, 42:69-78.

Buskirk, R. E. 1975a. Coloniality, activity patterns and feeding in a tropical orb-weaving spider. Ecology, 56:1314-1328.

Buskirk, R. E. 1975b. Aggressive display and orb defense in a colonial spider, *Metabus gravidus* (Araneae: Araneidae). Anim. Behav., 23:560-567.

Buskirk, R. E. 1981. Sociality in the Arachnida. Pp. 281-367, *In* Social Insects (H. R. Hermann, ed.). Vol. II. Academic Press, New York.

Eberhard, W. G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). J. Zool., 166:417-465.

Eberhard, W. G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. Evolution, 36:1067-1095.

Nentwig, W. 1983. The non-filter function of orb webs in spiders. Oecologia, 58:418-420.

Peters, H. M. 1969. Maturing and coordination of web-building activity. American Zool., 9:223-227.

Peters, P. J. 1970. Orb web construction: interaction of spider (*Araneus diadematus* Cl.) and thread configuration. Anim. Behav., 18:478-484.

Ramousse, R. and L. LeGuelte. 1984. Strategies de construction de la toile chez deux especies d'araignees (*Araneus diadematus* et *Zygiella x-notata*). Rev. Arachnol., 5:255-265.

Reed, C. F., P. N. Witt and R. L. Jones. 1965. The measuring function of the first legs of *Araneus diadematus* Cl. Behaviour, 25:98-119.

Riechert, S. E. 1985. Why do some spiders cooperate? *Agelena consociata,* a case study. Florida Ent., 68:105-116.

Risch, P. 1977. Quantitative analysis of orb web patterns in four species of spiders. Behav. Genet., 7:199-238.

Rypstra, A. L. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia, 59:312-316.

Rypstra, A. L. 1985. Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. J. Arachnol., 13:71-78.

Schoener, T. W. and C. A. Toft. 1983. Dispersion of a small-island population of the spider *Metepeira datona* (Araneae: Araneidae) in relation to web-site availability. Behav. Ecol. Sociobiol., 12:121-128.

Shear, W. A. 1970. The evolution of social phenomena in spiders. Bull. British Arachnol. Soc., 1:65-76.

Szlep, R. 1958. Influence of external factors on some structural properties of the garden spider (*Aranea diademata*) web. Folia Biol. 6:287-306.

Uetz, G. W. and J. W. Burgess. 1979. Habitat structure and colonial behavior in *Metepeira spinipes* (Araneae: Araneidae), an orb weaving spider from Mexico. Psyche, 86:79-89.

Uetz, G. W., T. C. Kane and G. E. Stratton. 1982. Variation in the social grouping tendency of a communal web-building spider. Science, 217:547-549.

Witt, P. N. and R. Baum. 1960. Changes in orb webs of spiders during growth (*Araneus diadematus* Clerck and *Neoscona vertebrata* McCook). Behaviour, 16:309-318.

Witt, P. N., C. F. Reed and D. B. Peakall. 1968. A Spider's Web. Springer-Verlag, New York. 107 pp.

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