AGGREGATIONS OF *NEPHILA CLAVIPES* (L.) (ARANEAE, ARANEIDAE) IN RELATION TO PREY AVAILABILITY

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ABSTRACT

Females of the species, *Nephila clavipes* (L.), sometimes build their webs in interconnected clusters. Aggregations in a Peruvian population of this spider were located in areas of high insect activity. This locale enabled individuals in aggregations to capture more prey than solitary individuals. Experiments with prey removal and prey supplementation verified that a high prey capture rate was essential in maintaining such groups. Agonistic interactions frequently preceded departure of a spider from a cluster. These data imply that high prey availability is a prerequisite for the evolution of more complex sociality in *Nephila* and other similar spider species.

INTRODUCTION

The evolution of sociality in various groups of animals has received much attention in light of the theory of natural selection (Wilson 1975, Maynard-Smith 1983 and references therein). Spiders are an unlikely recipient of this attention since they are voracious predators that frequently recognize conspecifics as prey. Nevertheless three levels of social interaction have been described for spiders based on some degree of tolerance, interattraction and cooperation (Shear 1970, Kullmann 1972). These social types include (1) colonial spiders that forage in interconnected webs, (2) spiders that aggregate only for the protection and rearing of young, and (3) spiders that share a common web in which they cooperate both in prey capture and in the rearing of young. Aggregate behavior in arachnids increases foraging efficiency, habitat exploitation, ease of mate location, and offers protection from predators and parasites (Buskirk 1975, Lubin 1974, Brach 1977, Rypstra 1979).

There appear to be two evolutionary pathways capable of producing some form of aggregation in spiders (Shear 1970, Kullmann 1972, Krafft 1979, Buskirk 1981). Along one route sociality results from an extension of parental care and the family unit. In the second pathway communal habits are the result of opportunism: selection favoring those individuals able to reap some ecological advantage from unintentional contact with conspecifics. In the study presented here, I focus on the evolution of intraspecific tolerance via that second pathway.

High prey availability is a likely prerequisite for the formation of aggregations in spiders. In spider species that maintain well-defined territories, field-measured nearest neighbor distances are smaller in populations that live in areas with high prey densities (Riechert 1978, 1981, Uetz et al. 1982). In situations where prey abundances are artificially maintained at exceptionally high levels territories disappear and both inter- and intraspecific tolerance appear in species that are normally solitary (Rypstra 1983). These factors make it tempting to hypothesize that occurrences of very high natural prey abundances make intraspecific competition for resources less necessary and allow the evolution of more amicable interactions between individuals.

The golden-web spider, *Nephila clavipes* (L.), is the focal species of this study. *Nephila* females build large webs in the open forest or edge habitats of tropical and subtropical America (Gertsch 1949, Peters 1954). The webs are fine-meshed circular orbs with varying amounts of barrier webbing surrounding them. An insect, detained by the sticky orb area, is usually subdued, wrapped and transported to the center of the web. Prey can either be cached or consumed immediately (see Robinson and Merick 1971, Moore 1977 for more details). Smaller spiders, called kleptoparasites, frequently occupy the barrier webbing and steal captured prey from the host spider (Vollrath 1976, Rypstra 1981).

I selected *N. clavipes* for this investigation of the relationship between food availability and sociality in spiders for two reasons. (1) Although adult females are usually solitary, in some habitats, individuals build webs adjacent to or intertwined with the webs of others (Shear 1970, Robinson and Merick 1971, Farr 1977). Understanding the circumstances when members of this species tolerate conspecifics in close proximity should provide insight into the factors that make possible the evolution of more advanced sociality. (2) Individuals of this species respond within one or two days to low prey consumption rates by relocating their webs (Rypstra 1981). Since long-term web site tenacity is apparently a reflection of an adequate prey supply, one would predict that webs remaining in close proximity are gathered around a favorable prey source.

METHODS

Aggregations of *Nephila clavipes* were studied in an area of subtropical moist forest in the Tambopata Reserve Zone, 29 km SSW of Puerto Maldonado, Department of Madre de Dios, Peru. Data were collected during June and July 1983. This time is the beginning of the dry season. Searches were made of all areas associated with major paths of the reserve. Each *N. clavipes* female found was marked with a drop of acrylic paint on her abdomen. If the barrier silk of two or more webs was contiguous the spiders were considered aggregated. Solitary spiders had webs with no silk connections to the webs of others.

I observed natural spider webs for two-hour periods at some time between 0900 and 1500 h. I recorded all activities of spiders and of insects that moved within ten cm of the webbing. Specific attention was paid to insect activity, prey capture rates, aggressive interactions in complexes, and kleptoparasite actions. Ten periods (20 hours) were spent with solitary individuals and 11 periods (22 hours) were spent with web complexes of four or more spiders. On three occasions I attempted to transfer kleptoparasites from the barrier webbing of one web to another.

An independent measure of prey availability was obtained via adhesive traps. Sheets of plastic (10 x 10 cm) covered with Tack Trap™ (Animal Repellents, Inc., Griffin, Georgia) were strung in the forest undergrowth for four-hour intervals. Sixty-four samples

were taken within a seven-day period. Thirty-two sheets were positioned 50 cm away from the capture surface of an individual in an aggregate and 32 sheets were placed 50 cm away from solitary webs. At the end of four hours the traps were collected and the captured insects were counted and categorized by order and size.

These observations allowed simple comparisons between the webs of solitary and aggregated individuals. In an attempt to reinforce any conclusions made about the formation and maintenance of aggregations, I conducted two experiments.

Experiments 1: Prey Removal.—A natural aggregate of six *N. clavipes* females located near a small stagnant stream was selected. Normal prey activity around this complex was determined by observation for four hours prior to manipulation. For ten consecutive days I visited this complex at 14:00 h. At that time I removed prey items, both living and dead, contained in the webbing. The diffuse nature of the barrier webbing made it possible to remove approximately 80-90% of the insects with little or no damage to the structure. I also noted changes in position or number of *N. clavipes* while observing the group for one hour. Prey removal was terminated after ten days. I returned to the complex on six subsequent days to determine if any other changes in the colony occurred. On these visits I plucked the webs near each prey item without removing them. This procedure should control for effects of web disturbance on colony integrity.

Experiment 2: Prey Supplementation.—*Nephila* females that have been starved for 48 hours will usually spin a web where they are released. Using this technique I created an aggregate of three spiders in an area for which both adhesive traps and insect observations indicated low prey activity. I visited this group daily at 10:30 h. for ten consecutive days. Ten to 15 live fruit flies (*Drosophila* spp.) were gently placed onto the capture surface of each *N. clavipes* web. I recorded the number and position of the spiders and observed their actions for one hour after prey addition. Supplementation was terminated after ten days. I returned to the site for six days to monitor the fate of this artificial aggregate. On these occasions I carefully touched the webbing in 10 places with a live insect but did not leave any additional prey in the trap.

RESULTS

Thirty-two *N. clavipes* females were located in the study area. Four natural aggregates accounted for 17 of these spiders (one with three members; two with four; one with six). The remaining 15 spiders were solitary.

During my observations *N. clavipes* spent about four percent of its time in web maintenance activities (clearing debris and repair). No difference is evident between solitary and aggregated webs (Table 1). Since all observations were of foraging spiders in completed webs no overall time/energy budget budget was determined.

Seventy-seven percent of the prey captured by *N. clavipes* in the Tambopata forest were small dipterans and hymenopterans (1-5 mm in total length). Many larger insects seemed to be capable of either avoiding the web or escaping before they were attacked. Overall, the webs captured 79% of the insects that contacted them (Table 1). The activity of insects in the small size range was significantly higher near aggregated webs than it was near solitary webs (Table 1). Individuals in aggregations captured more prey than did those in solitary webs (Table 1).

Two species of kleptoparasites in the genus *Argyrodes* Simon (Araneae: Theridiidae), occupy the barrier webbing of *N. clavipes* web in the Tambopata forest. From 0-12 *Argyrodes* fed on the prey of each host spider (Table 1). Similar numbers of *Argyrodes*

Table 1.—Comparative data collected for solitary (20 observation hours) and aggregate (22 hours) webs of *N. clavipes*. The presence of a * means there is a significant difference between the two groups using the Mann-Whitney U-test, p < 0.05.

	Solitary Webs $\overline{X} \pm$ S. D.	Aggregated Webs $\overline{X} \pm$ S. D.
Prey Activity/h (adhesive traps)*	3.9 ± 2.2	10.2 ± 3.4
Prey Activity/h (observed)*	7.6 ± 2.4	11.6 ± 3.8
Prey Captured/spider/h*	5.5 ± 1.4	10.3 ± 3.1
Capture Efficiency (captures/prey in web)	77.1 ± 7.5	82.5 ± 9.1
Web Maintenance (min/h)	2.6 ± 1.7	2.3 ± 2.0
Total Number of Kleptoparasites	3.2 ± 1.4	3.6 ± 1.9
Kleptoparasites/*Nephila**	3.2 ± 1.4	1.2 ± 0.9
Prey Lost to Kleptoparasites/*Nephila*/h	2.2 ± 1.7	1.4 ± 1.2
Prey Captured by Each Kleptoparasite/h*	2.2 ± 1.7	4.2 ± 1.4

occupied solitary and aggregated webs (Table). Consequently those individuals in colonies acquired significantly more prey (Table 1). *Nephila* females gave no indication that they were aware of the other spiders in the web. In no instance did they move into the barrier webbing or recover an item. Prey losses per *Nephila* individual were not significantly different between solitary and grouped spiders (Table 1). Kleptoparasite transplants were unsuccessful. *Argyrodes,* when introduced, retreated to a remote position or dropped out of the webbing entirely.

Aggressive interactions between *N. clavipes* females consisted of a rapid exchange of web jerks. During interactions individuals would orient toward the other spider with the anterior legs nearly straight out. In no instance did one female move onto the capture surface of the other. The spider would, however, move into the barrier webbing within three to four cm of another before either retreated. Only four interchanges were observed in natural aggregates. All of these were initiated by the same individual in one four-member colony. That individual had a capture rate of 5.5 prey per hour, which was the lowest recorded for any colony member.

Experiment 1.—The prey activity around this six-member colony was 15.4 insects/h which was the highest measured. Between six and 28 prey items were removed from each web surface daily during the experimental period (Table 2). On the third day of removal,

Table 2.—Data for individuals involved in prey removal experiment (exp. 1) including: prey capture prior to manipulation, average number of prey removed during the ten day experimental period, the day on which that individual departed from the colony, and whether that spider returned in six days after removal procedures were stopped.

Spider	Initial Capture Rate/ spider/hour	Number of Prey Removed $\overline{X} \pm$ S. D.	Day Left	Return?
1	7.5	9.0 ± 0.0	3	no
2	8.0	9.3 ± 2.5	4	yes
3	8.5	14.0 ± 3.5	5	no
4	12.0	20.4 ± 4.6	8	yes
5	13.0	21.6 ± 7.4	>10	—
6	13.5	22.0 ± 5.4	>10	—

Nephila individuals began to relocate away from the group (Figure 1). There is a correlation between the amount of prey captured by a spider in a given position and the time at which it relocated (Kendall's Tau = 0.933, p < 0.05) (Table 2). On days nine and ten a total of eight aggressive interactions took place between the two remaining females in the complex. After prey removal attempts were terminated, three *Nephila* females joined the aggregation (Figure 1). Two of the three were former residents of the colony (Table 2). The third previously occupied a solitary web about 12 m away. The number of *Argyrodes* in the aggregate declined form 12 to six during the experimental period.

Experiment 2.–The natural activity of prey around the artificially created aggregate was relatively low at 3.9 insects/h. During the period in which prey were added to the webs no *Nephila* females left and one previously unidentified female joined the group (Figure 1). After supplementation ceased, spiders began to disperse out of the area (Figure 1). Three aggressive interactions were observed on day 11. The initiator of these encounters was absent from the complex on day 12. Two acts of aggression were observed on day 13 and followed with the departure of the intiator by day 14. No kleptoparasites colonized these webs during this experiment.

DISCUSSION

Web construction constitutes a large energy investment on the part of a spider (Ford 1977, Prestwich 1977). Therefore it is essential that the web provide the spider with a suitable return in the form of insect prey. Many spiders, including *N. clavipes*, appear to make decisions about relocating their web based on their prey consumption rates (Turnbull 1964, Gillespie 1981, Rypstra 1981). Thus, it is not surprising that clusters of *N. clavipes* females should be associated with patches of prey. Even with this small sample size, the prey distributions, capture rates, and aggression levels recorded for the Peruvian population support this contention. Further evidence is provided by the relatively rapid dispersal of group members when food consumption was experimentally lowered (Figure 1). Similar results were obtained for the colonial orb-weaver *Metapeira spinipes* (Araneae; Araneidae) in Mexico. Uetz et al. (1982) found both the number of individuals remaining in a colony as well as the nearest neighbor distances within the group related to prey availability.

Agonistic interactions between *N. clavipes* females appear to be related to their prey consumption rate and to precede departure form a colony. Aggression between conspecifics at low prey levels is a likely factor operating to break apart aggregates. The metabolic cost of interactions coupled with a marginal prey capture rate could hasten the need for web relocation of juxtaposed individuals. At high prey levels aggression was not observed, presumably because competition for prey is reduced. One hypothesized prerequisite for a complex social existence to evolve is consistently high prey levels. Interestingly enough most social spiders live in tropical regions which typically have higher overall insect abundances than do comparable habitats in the temperate zone (Janzen 1973, Janzen and Pond 1975).

It has been suggested that spider's silk is a preadaptation for the evolution of social behavior in arachnids (Shear 1970). The silk acts as a communication network that precludes the need for physical or even visual contact during information transfer. The reactions of *N. clavipes* females to conspecifics in their web is clearly distinct from their reaction to potential prey items. During such agonistic encounters genuine communication occurs via an exchange of signals (Krafft 1982). Discrimination of web signals is key

to the development of any more complex social structure (Krafft 1982). However, the precise structure of an orb web seems to set limits on the amount of communal behavior that can evolve in a species such as *N. clavipes* (Burgess and Witt 1976, Burgess and Uetz 1982). The vibratory information that is transmitted in the circular capture surface of the web is focused on a single central point where there is only room for one spider (Burgess and Witt 1976). For this reason gregarious orb-weavers are usually colonial, maintaining individual webs within a matrix of interconnected webs (Buskirk 1981, Burgess and Uetz 1982, Krafft 1982).

It was not the purpose of this paper to evaluate if *N. clavipes* reaps any advantages directly form group participation. There is no difference in web maintenance expenses or capture efficiency between solitary and communal webs evident in the data presented here. No predation attempts were observed. Farr (1977), working with a population of *N. clavipes* in Florida, concluded that clumping was a stochastic phenomenon influenced by population density and the availability of suitable web sites. My data do not negate that contention in so far as a suitable site is one with a high prey yield for the spider. Farr (1977) also cited two disadvantages to colony formation in this species; lowered feeding efficiency and increased direct competition for mates. Prey capture rates did vary among the positions in Peruvian colonies (Table 2), however, all webs in the complexes were more productive than solitary webs (Table 1). In addition, experiments suggest that high prey capture rates are essential for continued group existence. This study generated no data on the mating hierarchies that might exist within *N. clavipes* colonies. However in
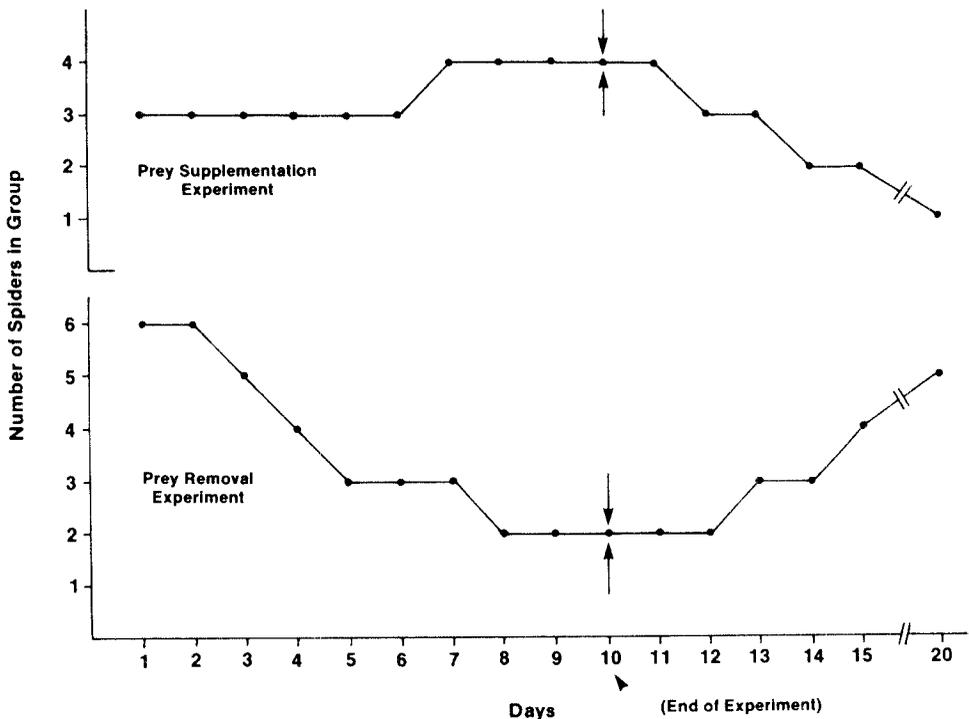

Fig. 1.—Number of *N. clavipes* in aggregations during experiments. In the prey removal experiment (bottom line) prey were removed from the webbing once a day for the first ten days. In the prey supplementation experiment (top line) 10-15 fruit flies were provided daily for each spider during the first ten days.

other studies of communal spiders, facilitation of sexual encounters was suggested as an advantage to group living (Lubin 1974, Valerio and Herrero 1977). The resolution of this question requires comparable data concerning the fitness of solitary females vs. the fitness of low-ranking females within an aggregation.

In a previous study on *N. clavipes*, the activity of kleptoparasites had a substantial affect on web site tenacity (Rypstra 1981). However in the few webs available for study here similar numbers of kleptoparasites occupy web complexes as live in single webs (Table 1). Based on that piece of information one would predict that aggregated individuals should loose fewer prey because the stealing events are spread over all of those in the group ("selfish herd effect" Hamilton 1971). No difference in prey losses to kleptoparasites by individual *Nephila* females were revealed between the two web situations (Table 1). Alternatively, if these few data reflect actual trends, kleptoparasites are experiencing significantly higher prey levels in *Nephila* aggregations (Table 1). The *Argyrodes* may be limiting their own density within webs in order to increase their food intake. My inability to alter *Argyrodes* densities in host webs made it difficult to test any of this more specifically.

Regardless of the actual position of *N. clavipes* in the evolutionary progression to spider sociality, the role of prey consumption in maintenance of aggregations in Peru has been established. The variability in spacing patterns that this species displays make it a valuable model system with which the situations that might allow for the appearance of more complex social interactions can be clarified.

ACKNOWLEDGMENTS

LITERATURE CITED

Brach, V. 1977. *Anelosimus studiosis* (Araneae: Theridiidae) and the evolution of quasisociality in Theridiid spiders. Evolution, 31:154-161.

Burgess, J. W. and G. W. Uetz. 1982. Social spacing strategies in spiders, Pp. 317-351, *In:* Spider Communication: Mechanisms and Ecological Significance (P. N. Witt and J. S. Rovner, eds.). Princeton Univ. Press, Princeton, New Jersey.

Burgess, J. W. and P. N. Witt. 1976. Spider webs: design and engineering. Interdisc. Sci. Rev., 1:322-335.

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

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

Farr, J. A. 1977. Social behavior of the golden silk spider, *Nephila clavipes.* J. Arachnol., 4:137-144.

Ford, M. J. 1977. Energy costs of the predation strategy of the web-spinning spider *Lepthyphantes zimmermanni* (Bertkau) (Linyphiidae). Oecologia, 28:341-349.

Gertsch, W. J. 1949. American Spiders. Van Nostrand-Reinhold, Princeton, New Jersey.

Gillespie, R. G. 1981. The quest for prey by the web-building spider *Amaurobius similis* (Blackwell). Anim. Behav., 29:953-954.

Hamilton, W. D. 1971. Geometry for a selfish herd, J. Theor. Biol., 31:295-311.

Janzen, D. H. 1973. Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology, 54:687-708.

Janzen, D. H. and C. M. Pond, 1975. A comparison, by sweep sampling, of the arthropod fauna of secondary vegetation in Michigan, England, and Costa Rica. Trans. Royal Entomol. Soc. London, 127:33-50.

Krafft, B. 1979. Organisation et évolution des sociétés d'araignées. J. Psychol., 1:23-51.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15-66, *In:* Spider Communication: Mechanisms and Ecological Significance (P. N. Witt and J. S. Rovner, eds.). Princeton Univ. Press, Princeton, New Jersey.

Kullmann, E. 1972. The evolution of social behavior in spiders (Araneae, Eresidae and Theridiidae). Amer. Zool., 12:395-405.

Lubin, Y. D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). Zool. J. Linnean Soc., 54:321-339.

Maynard-Smith, J. 1983. The evolution of social behaviour–a classification of models. Pp. 33-66, *In:* Current Problems in Sociobiology (King's College Sociobiology Groups, eds.). Cambridge Univ. Press, Cambridge.

Moore, C. W. 1977. The life cycle, habitat and variation in selected web parameters in the spider *Nephila clavipes* Koch (Araneidae). Amer. Midl. Nat., 98:95-108.

Peters, H. M. 1954. Estudios adicionales sobre la estructura de la red concéntrica de las arañas. Commum. Inst. Trop., El Salvador, 1:1-18.

Prestwich, K. N. 1977. The energetics of web-building in spiders. Comp. Biochem. Physiol., 54A:321-326.

Riechert, S. E. 1978. Energy-based territoriality in populations of the desert spider *Agelenopsis aperta* (Gertsch). Symp. Zool. Soc. London, 42:211-222.

Riechert, S. E. 1981. The consequences of being territorial: spiders, a case study. Amer. Nat., 117:871-892.

Robinson, M. H. and H. Merick. 1971. The predatory behavior of the goldenweb spider *Nephila clavipes* (Araneae: Araneidae). Psyche, 78:123-139.

Rypstra, A. L. 1979. Foraging flocks of spiders: a study of aggregate behavior in *Cyrtophora citricola* Forskål (Araneae; Araneidae) in west Africa. Behav. Ecol. Sociobiol., 5:291-300.

Rypstra, A. L. 1981. The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes.* Oikos, 37:179-182.

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

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

Turnbull, A. L. 1964. The search for prey by a web-building spider *Achaearanea tepidariorum* (CL Koch) (Araneae, Theridiidae). Canadian Entomol. 96:568-579.

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.

Valerio, C. E. and M. V. Herrero. 1977. Tendencia social en adultos de la Araña *Leucauge* sp. (Araneae, Araneidae) en Costa Rica. Brenesia, 10/11:69-79.

Vollrath, F. 1976. Konkurrenzvermeidung bei tropischen kleptoparasitism Haubennetzspinnen der Gattung *Argyrodes* (Arachnida: Araneae: Theridiidae). Entomol. Germ., 3:104-108.

Wilson, E. O. 1975. Sociobiology, the New Synthesis. Belknap Press, Cambridge.