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SOCIAL BEHAVIOR OF THE GOLDEN SILK SPIDER, *NEPHILA CLAVIPES* (LINNAEUS) (ARANEAE, ARANEIDAE)

James A. Farr [1]

Department of Biological Sciences
Florida State University
Tallahassee, Florida 32306

ABSTRACT

Web clumping by female *Nephila clavipes* is not a social phenomenon but rather a random process influenced by population density and number of suitable web sites. There is an uneven distribution of males in the webs of mature females, and it is believed that web clumping may actually be disadvantageous if a less attractive female constructs a web adjacent to a more attractive one. Larger females spin larger webs, so adjacent smaller females may suffer reduced feeding efficiency and hence reduced growth rate and lowered fecundity. Males attempt to mate with females when the latter are feeding, and in multiple-male webs, the males fight among themselves for females. If dominance hierarchies among males exist, it is predicted that they are only temporary, either because of inherent instability or because of male transcience.

INTRODUCTION

In his review of social phenomena in spiders, Shear (1970) mentioned the tendency of female *Nephila* spp. to share web support lines, and consequently suggested that *Nephila* might be semisocial. Comstock (1920) reported that adult *Nephila* males spin no web but live in the web of a female, and Archer (1940) observed that many webs contain more than one male. The present report examines the possibility of sociality in *Nephila clavipes* in more detail and investigates male-male interactions resulting from competition for females.

I asked three basic questions. First, is there a real tendency for females to construct webs in clumps, or is clumping a random process? Cohen (1971) analyzed casual group sizes in vervet monkeys and in man and found that group-size frequencies fit either a Poisson distribution or a negative binomial distribution with the zero-terms eliminated. If the group-size frequency distribution fits a zero-truncated Poisson distribution, size of a group does not influence its attractiveness, and it can be concluded that individuals do not seek other individuals, or that grouping is a stochastic process. In the present analysis, I attempt to fit an observed distribution of clump size frequencies to a zero-truncated Poisson distribution in an effort to detect deviations from randomness in support of the sociality hypothesis.

Is there an even distribution of males in the webs, or are some females preferred over others? The observation that some webs are inhabited by more than one male raises questions about male choice of females and about intermale competition for females. One

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[1] Present address: University of West Florida, c/o The U.S. Environmental Protection Agency, Sabine Island, Gulf Breeze, Florida 32561.

can ask whether certain females are more attractive than others, or if the uneven distribution of males is random. I analyzed frequency of occurrence of multiple-male webs and attempted to discover whether any particular quality of the females was correlated with male distribution and abundance.

Finally, I addressed the problem of intermale competition for females in multiple-male webs. Robinson and Robinson (1973) described the courtship of *Nephila maculata* and reported that although males typically wrap the females in strands of silk prior to mating, often this behavior is omitted and males will mount a female and copulate while she is feeding. They also reported that preliminary observations of *N. clavipes* indicated no wrapping of the female in silk prior to mating. I observed opportunistic mating in *N. clavipes* in webs with single males and then studied the responses of males in webs with more than one male. Agonistic encounters among males competing for females have been observed in the crab spider, *Diaea dorsata*, by Braun (1958), in the sheet-web spider, *Linyphia triangularis*, by Rovner (1968), and in *Nephila maculata* by Robinson and Robinson (1976), so I examined the possibility that similar behavior is exhibited by male *Nephila clavipes* in webs with more than one male.

Herein, I present evidence that clumping of webs by females is a random phenomenon and that males do aggressively contest for females. While it was ascertained that male distribution in female webs is not even, no particular attribute of females was found to account for this. The results are discussed in terms of the advantages and disadvantages of living in groups as directly related to reproductive success and fitness of *Nephila clavipes.*

MATERIALS AND METHODS

I observed natural populations of *Nephila* in two study areas. The first was in a hardwood forest surrounding a sink hole in Wakulla County, Florida, approximately 1.5 miles south of U.S. Highway 98 and approximately 2.0 miles east of the intersection of U.S. 98 and U.S. 319. This site was observed in July and August, 1974 and 1975, and the spider populations are hereafter referred to as Sink 1974 and Sink 1975. The second site was a hardwood forest directly across Appleyard Drive from Tallahassee Community College in Leon County, Florida, was observed in July and August, 1975, and is referred to as TCC 1975.

My initial sampling of the three populations involved a thorough, systematic search of the study areas and examination of all individuals encountered. For every web found, I measured the total length of the female (cephalothorax and abdomen), counted the number of attendant males, and recorded the number of other webs adjoining, sharing support lines, or with hubs less than 1.0 m apart. In 1975, after measuring the length of the female, I also measured the size of the webs at both sites. It should be noted that measuring total length gives only a rough estimate of relative size in this species, since the abdomen is highly distensible and varies in size according to reproductive condition and amount of food recently consumed. Measuring the length of the cephalothorax gives more reliable comparisons, but also involves closer measurement and a higher risk of disturbing the spider in its web. Since behavioral observations were performed on the same individuals, I chose total length and sacrificed precision for a lower probability of interfering with the natural behavior of the animals.

Behavioral observations were done as follows. If a female was feeding when first encountered and sexual behavior was observed, I recorded whatever behavior occurred. To elicit feeding behavior from the beginning, I used various species of crickets as prey. I

Table 1.–The frequency distribution of *Nephila clavipes* web clump sizes. The observed frequencies fit those expected from a zero-truncated Poisson distribution (X^2=5.749, d.f.=k-2=3).

Clump Size	Observed Frequency	Expected Frequency
1	49	45.90
2	17	20.54
3	4	6.13
4	3	1.37
5	1	0.25

simply tossed the cricket into the web below the hub in whatever area appeared to have the finest mesh and proceeded to make general notes on feeding behavior by the female and subsequent responses of the male(s). Although crickets are not the natural prey of *N. clavipes*, I detected no obvious differences in the social behavior of those females feeding on natural prey (various flying insects, particularly Lepidoptera and Coleoptera) and those feeding on crickets. Not every sequence was observed to completion.

RESULTS

I followed J. Cohen's (1971) analysis of casual group sizes in primates, used A. C. Cohen's (1960) tables for estimating the conditional Poisson parameter λ, and attempted to fit a zero-truncated Poisson distribution to the clump size data. A comparison of the observed and expected values of clump size frequencies (Table I) showed a good fit (X^2=5.749, d.f.=3). Thus, it can be concluded that clump size is random and the hypothesis that there is some intentional grouping or tendency to aggregate can be rejected. The Sink 1975 population and the TCC population were considerably less dense than the Sink 1974 population. During my initial sampling I found 19 clumps of one and two clumps of two at the Sink 1975 location, and 26 clumps of one and two clumps of two at the TCC 1975 site. This is further indication that clumping is not intentional but rather a random process facilitated in part by higher population densities.

It was noted in all three populations that there was not an even distribution of males in the webs of the females. In the Sink 1974 population there were many very small individuals with orb webs, and it was found that no webs constructed by spiders ⩽1.0 cm in total length contained mature males. Table II outlines the number of webs of individuals observed in each size class >1.0 cm and the number which contained at least one male. This analysis includes only the largest female of each clump and combines data for all three populations.

Robinson (pers. comm.) suggests that some individuals ⩽1.0 cm are probably immature males, that most females between 1.1 and 2.0 cm are immature, and that some females 2.1 to 2.5 cm are immature. There was no significant correlation between size of females ⩾2.1 cm and number of males in the web, although there was a high degree of variability in male number. Of 48 females sampled for number of males, 10 had no males, 25 had one male, eight had two males, four had three males, and one had six males. No obvious female characteristic appeared correlated with number of attendant males, and whether male number is random, like number of webs per clump, or there is some less obvious female feature determining attractiveness is unknown. It is interesting to note that males were found in many webs of immature females, a situation reported by

Table 2.—Observed size classes of the largest female *Nephila clavipes* in each clump at every site, including the number and percent observed with at least one attendant male.

Size class	N	Number with Males	Percent with Males
1.1 - 1.5 cm	29	6	20.7
1.6 - 2.0 cm	33	19	57.6
2.1 - 2.5 cm	20	15	75.0
2.6 - 3.0 cm	14	10	71.4
3.1 - 3.5 cm	8	6	75.0
>3.5 cm	6	5	83.3

Robinson and Robinson (1973). Robinson (pers. comm.) believes that this may be advantageous to the male in that it possibly ensures first mating once the female has matured.

I attempted to correlate size of the female's web with body length in the Sink 1975 and TCC 1975 populations. *Nephila clavipes* webs are incomplete orbs with an eccentric hub, so I could not measure diameter or area (see drawing in Levi and Levi, 1968, p. 65). Thus, I measured the distance R from the hub of the web to the lowest part of the orb. I found that body length, L, and web "radius", R, had the following relationships:

$$R=4.8+12.7\,L \quad (r=.887)$$

OR

$$R=17.8\,L^{0.82} \quad (r=.867)$$

Because the range of L was only 3.0 cm (1.1 cm to 4.1 cm), both a linear regression and a curvilinear regression of R on L were significant at the <.01 level. McNab (1963) found that home range size and mean species weight are exponentially related in several vertebrates.

I found eight different females with a single attendant male and that were in the act of feeding on flying insects when I encountered them. In each case, the male was seen to mount the female ventrally, Kaston's (1948) Position III, and copulate or attempt to copulate with the female. During the act of presumed insemination, the male tapped the emboli of the pedipalps against the epigynum of the female as described by Robinson and Robinson (1973). I saw no instances in which a female with a single male was not being mated while feeding.

In order to examine the entire behavioral sequence of mating, I chose 13 webs, each with a female and a single male, and introduced prey. In every case, as soon as the female moved from the hub of the web and attacked the prey, the previously motionless male began to move toward the hub. The predatory behavior of the female is very stereotyped and is described in detail by Robinson and Mirick (1971). After wrapping the prey, the female always returned to the hub to feed and assumed a head-down position in the web, at which time the male would mount the female and attempt to mate. In three of the 13 cases, the female chased the male away after the latter mounted, but in two of those, the male persisted in its attempts and ultimately appeared successful in mating. I was successful in eliciting the male behavior in 100% of my attempts. The entire sequence from the time the cricket was introduced to when the males ceased their activity lasted from 10 to 65 minutes.

Finally, I wished to examine behavioral interactions of males when competing for females in those webs with multiple males. At the Sink 1975 population I attempted to elicit sexual behavior in six webs with more than one male–three with two males and one each with three, four, and five males. Although I was able to elicit mounting and mating attempts by every male in single male webs, this was not the case with multiple-male webs, although at least one male attempted to mate in every multiple-male web. In each web with two males, only one male was successful in mating. In one instance, one male never moved after the female was fed. In a second case, the non-mating male moved to within 4 cm of the male that eventually mated, then retreated to a position approximately 30 cm above the hub of the web. In the third instance, both males moved to the hub simultaneously, and after a brief agonistic encounter, one male succeeded in chasing the other away.

In the three-male web I observed a peculiar series of events after the cricket was introduced. One male, that I will call male 1, went to the cricket and mounted and attempted to mate with the female while the latter was biting and wrapping the prey. When the female returned to the hub with the prey, male 1 rode on the former's back, where the male remained for most of the observation. Meanwhile, male 2 met the female at the hub, mounted, and mated. After about five minutes, the female gently brushed male 2 away. Male 3 approached the hub but was chased away by male 2 after a brief agonistic encounter. Male 2 attempted to mount the female twice more but was brushed away by the female. Finally, male 1 moved from the female's back to a position about 10 cm from the hub. Male 2 mounted the female, copulated, and dismounted. No further activity was observed.

In the four-male web, two males did not move for the first 30 minutes after prey introduction, then they only moved to within 15 cm of the hub. When the cricket was introduced, male 1 moved to the hub and mounted and mated when the female arrived with the prey. Male 1 remained there for 15 minutes before male 2, who had previously remained motionless, moved to the hub, mounted the female, and aggressively displaced male 1. During the encounter, male 1 lost a leg. Male 2 copulated for about five minutes, then male 1 returned, aggressively displaced male 2 from the female, and left without mating. Male 2 remounted, copulated, and left.

Finally, in the five-male web, one male remained motionless for the duration of the observations. There was much aggression among the other four. Initially, three males approached the female. Male 1 fought and chased off males 2 and 3, then mounted the female and mated. Males 2 and 3 fought each other twice during this time. Eventually, male 4 came to within 10 cm of the hub. Male 1 dismounted and chased away males 3 and 4. During this time, male 2 mounted the female, but he was aggressively displaced by male 1 after males 3 and 4 had gone to the periphery of the web. Male 1 remounted the female, copulated again, and at one point prevented male 3 from chasing itself off her. Approximately 45 minutes after the observations began, a male displaced male 1 from the female, mounted but left without copulating.

All aggressive interactions observed occurred in three seconds or less and involved what appeared to be a rapid physical beating of the opponent with the forelegs. I saw no type of threat display as has been observed in other species of spiders (Crane, 1949; Braun, 1958; Rovner, 1968). I could not determine whether there were attempts to bite the opponent, though I have observed such behavior when males are placed together in collecting vials, the result being death of the bitten individual. I could ascertain no obvious physical characteristics determining the outcome of any aggressive bout, as smaller males and males with fewer legs were often the victors. An investigation is currently underway to describe their agonistic behavior in detail and to study the influences on outcome of aggressive interactions.

DISCUSSION

Nephila clavipes is probably not a semisocial species as suggested by Shear (1970), since web clumping appears to be a stochastic phenomenon and entrance into a group is independent of group size. I suggest that there is a limited number of suitable sites for webs in any given habitat and that as the density of spiders increases, the probability that two or more occupy the same site increases. If females actively seek each other and build webs together, clump size frequencies would not be Poisson distributed.

There are obvious disadvantages to building a web near another female. First, a female that constructs a web adjacent to a more attractive female risks the possibility of not mating. Unlike other araneids, *N. clavipes* builds a permanent web, repairing damaged portions rather than constructing a new one (Gertsch, 1949). Thus, the presence of a more attractive female nearby could result in a long term reproductive disadvantage and reduction in fitness.

A second disadvantage of living in a group may be reduced feeding efficiency. Larger females build larger webs so have a higher probability of trapping flying insects. Several times I observed clumps of two or more females in which one female was feeding, and in all but one it was the largest female that was feeding. In the other case, a smaller female was eating a caterpillar, not the usual flying insects. If they are prevented from trapping more prey, smaller females might exhibit reduced growth rates. Since fecundity is usually exponentially related to size (Mota Alves and Bezerra, 1968; Swartz, in press; Abele, pers. comm.), a small difference in length represents a greater difference in fecundity. Also, immature females may exhibit delayed maturity as a result of reduced growth rate, and this in turn would reduce number of descendents and hence fitness.

It would seem that a male risks a serious reduction in fitness whenever there is more than one male in a female's web, and particularly when other females without males are nearby. If dominance hierarchies among males exist, I predict they are not stable and subordinate males have a good chance of ultimately being dominant. Logically, a subordinate male in a long-term stable hierarchy would seek another female with no males. A second alternative is that there are no lasting dominance hierarchies at all, that there is an agonistic contest among males whenever a female is feeding. However, this would not explain the observed instances of males not even attempting to approach the female. Finally, males may be transient and not remain long in one web. If this were the case, a male could ultimately mate with any female just by waiting long enough, particularly if prior residence in a web positively influences the outcome of agonistic encounters. It is known that male *Linyphia triangularis* remain in the female's web for no longer than two days, but they also do not tolerate the presence of a second male in the web (Rovner, 1968).

The actual copulatory behavior of *Nephila clavipes* was mentioned briefly by Robinson and Robinson (1973) in their analysis of the behavior of *Nephila maculata* in New Guinea. *N. maculata* males exhibit a ritualized courtship behavior including wrapping the female in strands of silk. My observations confirm their report that no such behavior is exhibited by *N. clavipes*; all copulatory behavior I observed was always preceded by the female capturing prey and was never preceded by ritualized male display behavior such as web vibration or wrapping the female. This opportunistic mating system parallels the highly ritualized food exchange in the courtship ceremony of the predatory balloon flies, family Empididae (Kessel, 1955), and the offering of prey to females by male *Pisaura mirabilis* during courtship (Bristowe, 1958). As in these examples, a *Nephila* female is less likely to eat an approaching male if the female has already captured a prey. Male balloon flies and *P. mirabilis*, however, present food to the female rather than waiting for the female to capture food.

From an ethological viewpoint, *N. clavipes* exhibits a unique signal-response system with one signal, the prey, eliciting a different response in males and females. If one employs Otte's (1974) scheme of functional and exploitative signal systems, the prey represents the signaler, the female represents the legitimate receiver, and the male is the illegitimate receiver. Males have evolved an exploitative, deceitful behavior as a response to the risk of intraspecific, intersexual predation.

In summary, the phenomenon of clumping in *Nephila clavipes* is not a result of semisociality but rather a stochastic phenomenon influenced by population density and availability of suitable sites for webs. As further evidence against the hypothesis of sociality, females in clumps of two or more are at a possible selective disadvantage because of differences in attractiveness to males and lowered feeding efficiency. Number of males per web is variable, and where there are two or more males, they aggressively contest for females at the risk of injury or death. It is predicted that if dominance hierarchies among males exist, they are temporary, and that males may remain in webs for only a short time. Further studies of ritualized aggression and dominance hierarchies in *Nephila* are in progress.

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