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ANTIPREDATOR BENEFITS OF SINGLE- AND MIXED-SPECIES GROUPING BY *NEPHILA CLAVIPES* (L.) (ARANEAE, TETRAGNATHIDAE)

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ABSTRACT. The golden silk spider, *Nephila clavipes* (L.), is known to live both solitarily and in single-species aggregations. In Veracruz, Mexico, *N. clavipes* is also found in association with the colonial orbweaver *Metepeira incrassata* F.O. Pickard-Cambridge (Araneae: Araneidae). This study compared the frequency of predation attempts on solitary, intraspecifically aggregated and colony associated *N. clavipes*. Solitary *N. clavipes* suffered greater relative predation than those in single-species groups or those associated with *M. incrassata* colonies. We also compared the distance at which the three categories of *N. clavipes* were able to detect and respond to a simulated predation attempt. Both intraspecifically grouped and colony associated *N. clavipes* had significantly greater response distances than did solitary individuals, indicating that they could respond to a predation threat sooner. These data support predictions that grouped spiders may benefit from lower predation and/or an early warning system.

Although spiders, as predators, have been well studied, evidence for the types and especially the frequencies of predation on spiders is lacking. Predation rates on solitary spiders may be quite high (Askenmo et al. 1977; Gunnarsson 1983), especially in tropical areas (Rypstra 1984; Vollrath 1985). There is evidence that spider webs are irritating to vertebrate predators such as birds (Horton 1980; Eisner & Nowicki 1983), and it has been suggested that the dense webbing of colonial spiders might act to deter predation (Lubin 1974; Robinson & Robinson 1976; Rypstra 1979). It has also been hypothesized that colonial spiders may benefit from an "early-warning system", in which the intertwined webbing transmits alarm signals from other spiders or vibrations from predators, causing spiders to take evasive action (Lubin 1974; Rypstra 1979; Uetz 1985). To date, however, actual evidence for antipredator benefits in colonial spiders is limited (Spiller & Schoener 1989).

There are several ways that animals in groups can avoid predation: shared vigilance and early warning signals may increase the chances of predator detection (Pulliam & Caraco 1984); reduction of individual risk as a result of being one of many possible prey present (Hamilton 1971); predator deterrence arising from collective mimicry or aposematism (Morse 1980); group defense, such as mobbing. While the above ideas were developed with regard to single-species grouping, reduction of predation frequency has also been reported in a variety of mixed-species groups (reviewed in Morse 1977 and Barnard & Thompson 1985). However, it is also possible that individuals in mixed-species groups might experience a unique disadvantage with respect to predation if they are different in appearance from the majority of the group. There is evidence that odd group members are selectively preyed upon in heterospecific groups (Mueller 1975; Milinski 1977; Ohguchi 1978).

The goal of this study was to determine whether predator avoidance benefits exist for spiders in heterospecific groups. Mixed-species associations have been noted to occur between colonial web-building spiders and other spider species (Lubin 1974; Sabath et al.1974; Bradoo 1972, 1979; Rypstra 1979; Berry 1987; Lopez 1988; Hodge 1990). Spiders in the genus *Nephila* (Tetragnathidae) often form intraspecific aggregations (Shear 1970; Moore 1977; Farr 1977; Rypstra 1985; Higgins 1988). Other species of web-building spiders associate with *Nephila* groups (McCook 1890; Strusaker 1969; Yoshida 1988) and *Nephila* have been found in association with colonial orbweavers (Jackson 1986; Hodge 1990).

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Because they are found solitarily, in single-species and in mixed-species groups, *Nephila* are ideal for comparing of the costs and benefits of these three different living situations.

METHODS

We studied predation on a natural population of female *Nephila clavipes* (L.) (Araneae: Tetragnathidae) on the grounds of the Hotel Posada Loma, Fortin de las Flores, Veracruz, Mexico, where they exist solitarily, in single-species groups and in association with a colonial orb-weaving spider, *Metepeira incrassata* F.O. Pickard-Cambridge (Araneae: Araneidae) (Hodge 1990). The habitat is classified as high semi-evergreen selva (Gomez-Pompa 1977) and the study site consisted of approximately 1.5 hectares of unenclosed botanical gardens. Evidence of possible predation was recorded during daily prey capture observations (Hodge 1990) performed between August 18–September 9, 1988. During these observations, groups and individuals on the grounds were inspected during the morning, and again before dark. A predation attempt was assumed to have occurred if an individual was present on her web between approximately 0600 h and 1200 h, but was absent from the web and the area immediately surrounding the web before nightfall, and evidence of predation was found. Such evidence consisted of the presence of a large hole in the orb-web, which is a reliable sign of predation attempts by birds (Higgins, in press). It is possible that such damaged webs could also be caused by large insects impacting the web and then escaping. However, in such cases the spider usually rebuilds all or part of the web rather than relocating. When *Nephila* voluntarily relocate, they usually do so during the night, after ingesting the orb web (Horton 1982; Higgins, in press; Hodge, pers. obs.).

The average population size of each of the three categories of *N. clavipes* was estimated from three different censuses performed during the study period (Table 1). The number of *N. clavipes* in each category in the area of the predator attack observations was recorded during each census. Relative predation on each category of *N. clavipes* was estimated by calculating the percentage which disappeared due to apparent predation. The mean group size of intraspecific groups in the population during the study period was 3.76 ± 2.34 (n = 20 groups).

To test the "early-warning" hypothesis, predation attempts were simulated by disturbing webs of arbitrarily chosen individuals by tapping with a stick (the "pencil-poke" method: Tolbert 1975). Tapping was initiated as far from the center of the orb as possible, usually where the web was attached to vegetation. If no response was elicited, the disturbance was moved toward the orb at 1 cm intervals until a response was elicited, or until the center of the orb (where the spider sits) was reached. The distance (cm) from the disturbance at which each spider performed an antipredator response was recorded. Behaviors scored as antipredator responses were: drop from web, run off web or shake web. All of the web disturbances were performed on a single day (September 12, 1988) to control for possible effects of differences in temperature or other environmental variables on spider response. The conditions were cloudy, so no spiders were under heat stress, and the ambient temperature was 24 °C. The mean size of intraspecific groups involved in these manipulations was 3.28 ± 1.98 (n = 7 groups). The size of the *Metepeira incrassata* colonies ranged from approximately 500–1000 spiders.

Table 1.—Estimated relative predation attempts on solitary, single-species and mixed-species associated *N. clavipes* between August 18 and September 9, 1988 (estimated population size = mean number of individuals in each category based on three censuses ± standard deviation).

	Estimated population size	Evidence of predation attempts
Solitary individuals	36 ± 2.08	12 (33%)
Intraspecific groups	77 ± 2.52	8 (10%)
Mixed-species groups	43 ± 5.13	4 (9%)

RESULTS

Solitary *N. clavipes* experienced a greater percentage of predation attempts than did single-or mixed-species groups, which had similar levels (Table 1; G-test, $P < 0.01$). Response distances of solitary *N. clavipes* subject to the mock-predation disturbance were significantly less than those of individuals in single- or mixed-species groups (Table 2; Kruskal-Wallis, $P < 0.05$). The primary difference was between grouped webs and solitary webs ($P < 0.05$; non-parametric multiple comparison procedure, Zar 1984); there was no difference between response distances of

Table 2.—Comparison of distances at which response was elicited to simulated predation by solitary, single-species and mixed-species associated *N. clavipes* (response distance = mean ± standard deviation; n = number of individuals in each category).

	Response distance (cm)	n
Solitary individuals	21.5 ± 26.7	20
Intraspecific groups	41.9 ± 25.3	26
Mixed-species groups	38.4 ± 33.6	19

single- or mixed-species groups (Table 2). Thus, there was no early-warning benefit to *N. clavipes* associated with groups of *M. incrassata* exceeding that of individuals in single-species groups.

DISCUSSION

These data support predictions that grouped spiders benefit from lower predation and/or an early-warning system. They do not, however, support the hypothesis that odd group members (i. e., *N. clavipes* in *M. incrassata* colonies) are selectively preyed upon. *Nephila* in both single- and mixed-species groups suffered a lower frequency of predation attempts and had greater response distances than solitary individuals. However, there was no evidence that individuals living in *M. incrassata* colonies had any greater advantages than those living in single-species groups. The similarly low predation frequency on both types of groups may be related to hesitation on the part of wasp or bird predators to attack grouped webs. An alternative explanation, however, may be related to a foraging related benefit of group living. *Nephila* in single and mixed-species groups capture significantly more prey biomass, and hence are larger in body size than the solitary individuals (Hodge 1990). Depending on the size of the predator, there may be limits to the size of spider that they will attack.

The greater response distances observed for grouped webs was most likely a function of more silk between the "potential predator" and the spider than exists in solitary webs, and thus a greater distance over which vibrations could be detected. In natural situations, individual escape behaviors might transmit vibrations and elicit evasive behavior among other members of the group. Two factors may account for the lack of difference in response distance between single- and mixed-species associated *N. clavipes*. First, it was only possible to use somewhat peripheral spiders as focal animals in mixed-species groups (which typically contained 500–1000 spiders) to avoid reaching into and partially destroying the colony. The amount of silk between the experimenter and the spider was therefore probably not much different in single-species or mixed-species situations. In addition, even if the distances had been different, there may be an upper limit to the distance that disturbance vibrations can be transmitted before they attenuate. Therefore, there may be some upper limit of group size beyond which no additional early-warning benefit will accrue. However, the possibility does exist that had a different experimental protocol been used a slightly greater response distance may have been detected for *N. clavipes* in *M. incrassata* colonies, since these colonies do have more silk, and hence, a greater potential distance for signal transmission.

Existing evidence suggests that foraging benefits most likely select for tolerance and coloniality in spiders (Lubin 1974; Rypstra 1989; Uetz 1988, 1989) and conditions of very high prey density favor the formation of mixed-species association as well (Rypstra 1979, 1983; Hodge 1990). Large spider colonies may actually be a liability with respect to predation since they potentially attract more egg-sac parasites (Lubin 1974; Rypstra 1979; Buskirk 1981; Smith 1982; Heiber & Uetz 1990). However, the results of this study indicate that some antipredator benefits may result from group-living. While not necessarily the driving force behind the evolution of social tendencies in spiders, such antipredator benefits may, in some cases, be an advantageous fortuitous effect of both single- and mixed-species associations between web-building spiders.

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