An Association between Two Neotropical Spiders (Araneae: Uloboridae and Tengellidae)

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ABSTRACT

An interspecific association between two spider species (Araneae, Uloboridae and Tengellidae) was studied over a six-week period at an Atlantic lowland wet forest site in Costa Rica. The uloborid *Philoponella vicina* builds orb webs among the frame lines of the platform web constructed by *Tengella radiata* Kulczynski, the much larger tengellid species.

Experiments with marked *P. vicina* determined that these uloborids actively choose to build in *T. radiata* webs. Studies of possible advantages the uloborid may derive from inhabiting the web of the tengellid showed that: 1) "Associated" uloborids persisted at a web site significantly longer than "solo" uloborids; 2) prey capture was significantly greater for the "associated" uloborids than for the "solo" spiders. The association of *P. vicina* and *T. radiata* appears to be commensal.

As SOLITARY PREDATORS, most spiders are intolerant of conspecifics; even potential mates are sometimes treated as prey. While conspecific associations are known for sub-social, communal, and social spiders (Muma and Gertsch 1964; Pain 1964; Darchen 1965; Dennis 1965; Lubin 1974; Buskirk 1975; Brach 1977; Burgess 1976, 1979; Jackson and Joseph 1973), reports of interspecific associations in the literature are rare and anecdotal (reviewed by Kaston 1965). Within the family Uloboridae, however, tolerance of conspecifics is common (Muma and Gertsch 1964; Eberhard 1971; Buskirk 1981), and several species are known to form commensal and slightly parasitic associations with other spiders (Struhsaker 1969, Bradoo 1972, Opell 1979). I report here on a neotropical association between *Philoponella vicina* O. Pickard-Cambridge, a uloborid orb weaver, and *Tengella radiata* Kulczynski, a tengellid platform weaver, and present evidence that the association is advantageous to the uloborid.

This study attempted to test the nature of the association and addresses the following questions: 1) Do *P. vicina* actively select *T. radiata* webs as web sites? 2) Is prey capture in "associated" uloborids higher than in unassociated ("solo") ones? 3) Do tengellid webs offer greater protection from predation than other sites? 4) Do tengellid webs offer uloborids potential site positions in areas where they could otherwise not build?

The interspecific association observed may be the result of an active search by uloborids for tengellid webs, or it may result from higher mortality of uloborids which establish themselves outside tengellid webs, or both. An affirmative result of a test of (1) above would indicate that uloborids are using some cue to locate the tengellid webs, and that the association is not merely the result of differential mortality of uloborids. If site selection is an active process in uloborids, one may presume that the spiders derive some advantages in inhabiting the web space of the tengellids. Tests of questions (2), (3), and (4) were designed to determine whether correlates of fitness, such as lower predation or higher rate of prey capture, differ significantly between uloborids building webs inside and outside of tengellid webs.

DESCRIPTION OF STUDY SITE AND ORGANISMS

The study was conducted at the Organization of Tropical Studies Field Station at La Selva, near Puerto Viejo, Costa Rica (Heredia Province), from 12 March to 25 April 1979, just prior to the rainy season. La Selva is a tropical lowland wet forest (Holdridge 1967). Spider webs used in the study were located in the primary forest along the Research Trail and in the Arboretum, an area cleared of forest understory plants. Voucher specimens of *Tengella radiata* and *Philoponella vicina* were deposited in the Museum of Comparative Zoology, Harvard University.

Philoponella vicina builds a horizontal orb web of cribellate silk, characterized by a reticulate, closed hub, a silk stabilmentum, and a zig-zag perimeter (for a detailed description, see Peters 1953). These spiders are small (5-15 mm total body length). *Tengella radiata* with which they associate builds non-sticky platform webs in tree buttresses, rotting stumps, and similar habitats. The platform narrows into a funnel retreat at the far end. A large barrier web, which may be four or five times the platform diameter, extends above the platform. The size of *T. radiata* varies from 10 to 20 mm (total body length), and can be estimated from the diameter of the funnel. Uloborids may build their orb webs between the lines of the tengellid barrier web, on the side of the platform, or across the width of the platform itself. The webs of mature tengellids are large enough to accommodate several uloborids, and up to nine *P. vicina* have been found occupying a single host web. "Solo," unassociated uloborids are also found building webs in tree stumps, along tree buttresses on the ground, or in low vegetation. Such *P. vicina* are often aggregated in groups of two or three. These aggregations appear to be pre-social, as the only interactions I observed between *P. vicina* conspecifics were two mating attempts.

An earlier study showed the association to be species specific and widespread. Coddington and Fincke (unpublished, 1979) sampled 68 buttressed trees in the primary forest of La Selva. Of the 102 *P. vicina* found in the buttresses, 78 percent inhabited the web space of *T. radiata.* Of the 107 tengellids sampled, 51 percent had at least one uloborid associated with it. This distribution deviates significantly ($p < 0.005$, d.f. $= 1$) from the expected if one assumes the null hypothesis that the distribution of each species is independent of the other.

METHODS

GENERAL.—*Philoponella vicina* webs were dusted with a thin layer of cornstarch to make them more visible. Spiders were marked with a drop of fluorescent paint on the dorsal abdomen. Adult males and females and larger immatures were used. Smaller immatures are almost impossible to mark efficiently, and they build small, sheet-like webs which are easily overlooked. A small population of "associated" and "solo" uloborids and their host was maintained in the laboratory for behavioral observations. Specific experiments are described below.

SITE CHOICE.—To determine whether *P. vicina* actively choose to build in the host webs, choice experiments were conducted using a total of 138 *P. vicina* randomly selected from both "associated" and "unassociated" webs. Marked individuals (a random selection of mature males, females, and immatures, scored large, medium, or small according to their relative size) were dropped singly on a buttress ridge, on one side of which was a tengellid web; on the opposite side, tengellid webs were absent. Both sides had previously been cleared of all uloborids. In half of the tests, the tengellid web was on the right side, and in half, it was on the left side of the buttress. The control group consisted of single uloborids placed on buttresses separating two tengellid-free sides. All of the buttresses were then checked 24, 48, and 72 hours after the spider's release, and the position of the recovered uloborid was recorded.

To insure further that I had not biased the number of experimentals later found in tengellid webs as opposed to outside of their webs, I released marked *P. vicina* in buttresses of trees unoccupied by tengellids or uloborids (assumedly "unfavorable" sites for both species) and on tengellid webs previously cleared of all other uloborids.

SITE TENACITY.—As recording observations of predation *per se* in the field would be too inefficient, I chose to monitor site tenacity as an indicator of predation, on the assumption that wandering spiders are more susceptible to predators than those on webs (on several occasions, I witnessed predation on webless *P. vicina*). A spider which remains at a site could not have been eaten, while a spider that disappears from a site may have been eaten.

Every three days for a six-week period, 26 "solo" and 52 "associated" *P. vicina* were checked. As more uloborids were discovered, they were likewise monitored, bringing the total sample up to 96 "solo" and 91 "associated" uloborids. Absence of a spider for a period greater than six days was scored as a disappearance. Because of the mortality and damage involved in capturing and marking spiders, I chose not to mark these spiders. Very often, marking them with paint seemed to induce molting. Over a period of several weeks, the necessary re-markings would have seriously reduced my sample size. Since uloborid webs disintegrate within about 24 hours if left untended, the presence of a particular spider was inferred from the presence of a web at a particular site. Mature males, which do not build webs, were relatively easy to find because they are yellow and because they were usually near the web of a mature female. Females guarding egg cases likewise do not build webs, but they are conspicuous by their size. While monitoring could not distinguish between a spider which disappeared and one which had colonized the same site within six days, such incorrect scorings were probably few, since it seems unlikely that many such coincidental replacements would occur. All web sites were identified by number and marked with a small piece of colored plastic tape. Relatively more time was always spent relocating the "solo" uloborids, as they were easier to overlook, since their webs could be scattered about a larger area in the vegetation, and they sometimes changed their web position slightly.

PREY CAPTURE.— Prey capture by 66 "associated" and 44 "solo" uloborids was recorded at regular intervals (from 45 minutes to 2½ hours) between 09:30 and 17:00 over a nine-day period. The number of prey items both held by the spider and wrapped in the web were counted. It was easy to distinguish between new prey and previously counted prey in the process of being consumed since a uloborid requires an hour or more to suck out a prey item the size of a fruit fly, and the prey becomes visibly smaller in the process. While this method did not sample all the prey an individual might catch during a day, sampling of "associated" and "solo" uloborids was at equal intervals of time, and at approximately the same time of day, enabling a comparison of relative differences in capture rates. In addition, rough measurements of total body length (legs extended in the resting position on the web) were taken of 38 "solo" and 60 "associated" *p. vicina.*

Prey capture of associated uloborids may be increased due to some feature inherent in the tengellid web site, or due to increased density of uloborids packed within the limited space of the tengellid web. In order to determine the effect of the presence of conspecifics on prey captures, average prey capture/individual/day was plotted against the number of uloborids present at "solo" and "associated" sites. A site for "solo" uloborids was loosely defined as a one-cubic-meter space around a uloborid web. As even "solo" uloborids are often clumped in their distribution, the maximum number which were located within a cubic-meter space were recorded as being at the same site. For "associated" uloborids, the site was defined as the area of the tengellid web.

RESULTS

SITE CHOICE.—The results in table 1 indicate that *P. vicina* actively choose to build in tengellid webs. A chi-square goodness-of-fit test showed that there is only a slightly greater probability of finding an experimental spider given a choice of building in a tengellid web than a control spider released on a buttress between two tengellid-free sides ($p < 0.25$). A chi-square test conducted only on those experimental spiders found after three days showed that the position chosen by the uloborids differed significantly from a random 50-50 distribution between the two buttresses ($x^2 = 24.4$, $p < 0.005$, d.f. = 1). Of the experimental spiders found, 22

TABLE 1. *Results of choice experiment. a) Experimentals refer to uloborids placed on a buttress on one side of which was a tengellid web, the other side being free of tengellid webs. Controls were placed on buttresses dividing two tengellid-free sides. Chi-square test* ($x^2 = 2.1$, d.f. = 1, $p < 0.25$) *shows that the difference between the number of unrecovered spiders in the experimental and control groups was not significant. b) Of the experimentals found, significantly more were recovered from tengellid webs* ($x^2 = 4.5$, $p < 0.05$).

a)	Uloborids found (n)	Uloborids not found (n)
Experimentals	32	25
Controls	16	23
b)	**Observed**	**Expected**
Uloborids found in tengellid webs	22	16
Uloborids found outside of tengellid webs	10	16

TABLE 2. *Comparison of recapture success of uloborids in different release sites. A 2 x 4 goodness-of-fit test showed no significant difference in the numbers of unrecovered spiders from the four release sites* ($x^2 = 3.8$, d.f. = 3, $p < 0.5$, n.s.).

	Choice test: experimentals' site	Choice test: controls' site	Unoccupied buttresses	Amaurobiid webs
Spiders found (n)	32	16	7	18
Spiders not found after three days (n)	25	23	11	13

(69%) were occupying tengellid webs, as opposed to 8 (25%) which had built in the buttress with the tengellid web but outside of the web. Only two (6%) built in the empty buttresses. These results (table 1b) are significant at the 0.05 level ($x^2 = 4.5$, d.f. = 1).

The results from the additional release sites, table 2, show that there was no significant difference in the number of uloborids which were never recovered, regardless of the release site. In any group of uloborids released, 50 percent disappeared (due to predation, mortality from the handling or marking, or migration), shed the paint mark by molting, or consistently eluded my search. I therefore concluded that the results of the choice experiment were not biased due to the greater ease in locating *P. vicina* in *T. radiata* webs as opposed to finding them anywhere in the buttress space.

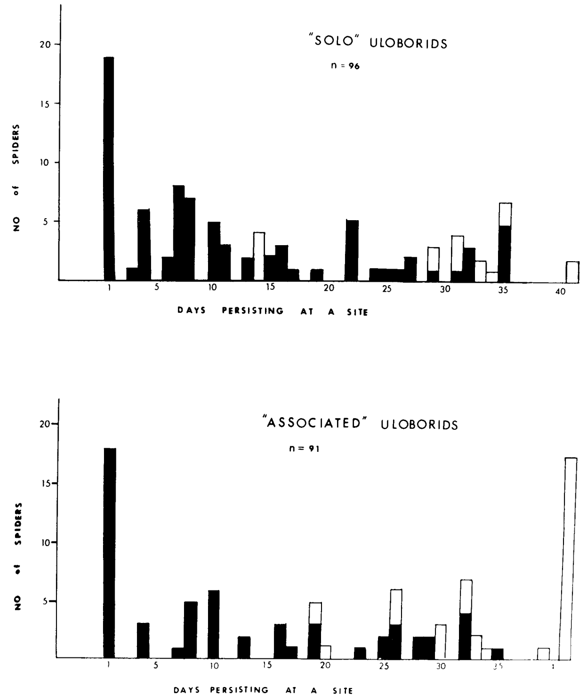

FIGURE 1. Site tenacity of "solo" versus "associated" uloborids over a 41-day period. Shaded bars represent spiders which disappeared during the study period. Unshaded bars represent spiders still persisting at the original site when the study was terminated. "Associated" uloborids persisted significantly longer than "solo" ones ($p < 0.03$, Mann-Whitney U Test).

SITE TENACITY.—Figure 1 presents the duration of the "solo" and "associated" uloborids at the site where they were originally found. Analysis by a Mann-Whitney U Test showed that the difference in site persistence between the "associated" and "solo" groups is significant at the 0.03 level, with "associated" *P. vicina* persisting at a site longer than "solo" individuals. Spiders in both groups which persisted for the entire study (16 March-25 April) were scored for 41 days, even though they might have persisted longer. Spiders found after 16 March which were still present on 25 April were discounted from the analysis as they were not observed for the entire 41-day period and did not disappear during the time observed.

PREY CAPTURE.—"Associated" spiders caught a mean of 0.41 prey items per day while "solo" spiders averaged 0.32 prey items per day (fig. 2). This difference is significant at the 0.01 level (Wilcoxon Matched Pairs Signed Ranks Test, $T = 3$). "Associated" uloborids were found to be significantly larger than their "unassociated" conspecifics. Mean size was 6.9 ± 0.37 mm for "associated" spiders and

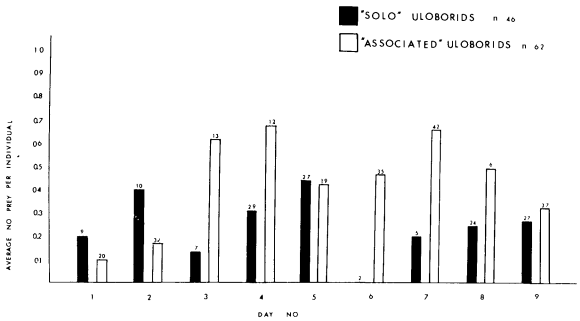

FIGURE 2. Prey-capture rates of "solo" and "associated" uloborids on nine days. Numbers above the bars indicate the sample size used to determine the averages for each day. Prey capture by "associated" uloborids was significantly higher than by "solo" ones ($p < 0.01$, Wilcoxon Matched Pairs Signed Rank Test, $T = 3$).

5.8 ± 0.51 mm for "solo" spiders ($p < 0.003$, Mann-Whitney U Test). The number of conspecifics present at "associated" sites positively correlated with prey-capture rates, while at "solo" sites, no such correlation was found. Spearman Rank correlations, corrected for ties, gave a correlation of $r_s = 0.36$, significant at the 0.05 level, for "associated" spiders and an insignificant correlation of 0.15 for "solo" spiders (fig. 3).

DISCUSSION AND CONCLUSIONS

Site choice, site tenacity, and enhanced prey capture show that this uloborid-tengellid association is advantageous to the uloborid and is not merely the coincidental overlap of two species utilizing a particularly attractive site. The majority of *P. vicina* recovered in the choice experiments were found within 24 hours. Since webs were most likely built the morning after release, spiders would not have had time to sample prey density within the buttress, and thus could not have been responding to any increased prey density which might be around tengellid webs. One assumes that tengellids select sites where their prey capture is at least adequate. *Tengella radiata* is nocturnal, feeding primarily on cockroaches, crickets, and other insects which crawl or hop onto the platform. *Philoponella vicina*, on the other hand, is primarily diurnal, preying upon tiny beetles, fruit flies, other small flying insects, and ants. Even if tengellid sites also happened to be adequate for the capture of uloborid prey, this fact alone would not explain why uloborids chose to inhabit the web space of a much larger predaceous spider, rather than the surrounding area.

While the means by which *P. vicina* locates ten-

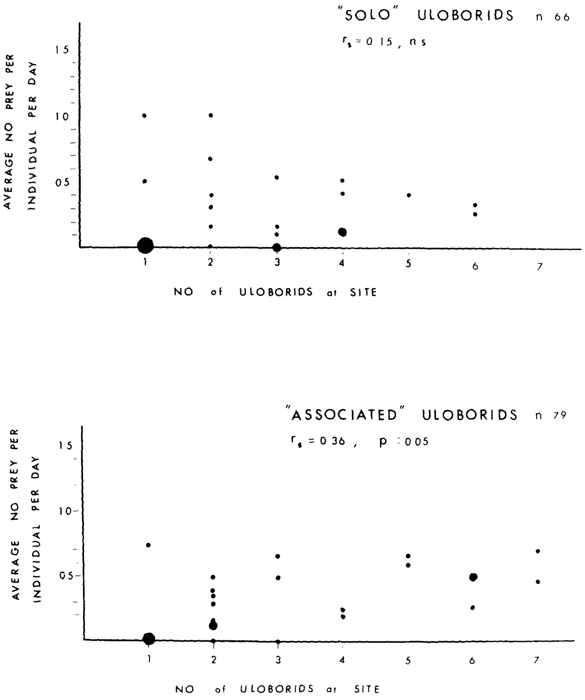

FIGURE 3. Prey-capture rates plotted against number of conspecifics at a site. Smallest dot represents one site, the largest dot represents four sites, the two intermediate sizes represent two and three sites. Spearman Rank correlations show that prey-capture rates of uloborids "associated" with a tengellid vary significantly with the number of uloborids at a site while prey-capture rates of "solo" uloborids do not.

gellid webs is not known, it is possible that chemical cues are involved. Tietjen (1977) has shown that male wolf spiders are able to detect conspecific female draglines by tactile and pheromonal cues. *Philoponella vicina* may use similar cues to locate tengellid webs as well as aggregations of conspecifics.

If tengellid webs provided only attachment sites for *P. vicina* webs, then one would expect to find uloborids occupying abandoned tengellid webs whose lines were still intact. As this is seldom the case (the few I found were in newly abandoned webs and these uloborids left after several days), it seems reasonable to assume that uloborids are responding to features other than attachment structures.

The number of *P. vicina* not recovered in the choice experiments is about 50 percent in all of the individual tests. While some recapture failures were probably due to observer oversight and spider migration, predation may be a major cause. Several times I saw a marked spider fall prey to an *Anolis* lizard within minutes after being released on a buttress. *Anolis* lizards and *Dendrobates* frogs are common on the lower trunks of trees, and I suspect that many of the spiders were preyed upon before they were able to find retreats. Upon release on a buttress, a uloborid would walk upward until it found a retreat (under a vine, on an epiphyte, etc.) and remain there. As I did not watch a released spider for more than 20 minutes, I do not know exactly when it began searching for a web site, though I suspect it waited until morning when uloborids normally build new webs. In his study of site selection, Turnbull (1964) found that the orb weaver *Achaearanea tepidariorum* likewise initially remained in a retreat, building a web 12-36 hours after release. Even if one assumes that those experimental spiders released moved away from the tree entirely, 44 percent of the experimental spiders released were recovered from tengellid webs, a finding which indicates that site selection is a nonrandom process.

The data on site tenacity reflect the sum of migration and mortality of "associated" and "solo" uloborids. Much of the disappearance of *P. vicina* in the field was probably due to some factor other than migration to a site of greater prey abundance. While it is known that orb weavers change sites if prey at that site are inadequate (Turnbull 1964) or if the web is badly damaged (Eberhard 1971, Enders 1975), once a favorable spot is found, they are likely to move very little. "Associated" and "solo" *P. vicina* kept in the lab showed little or no change in site position over the six-week study period, during which time they had a constant supply of *Drosophila* prey. If prey abundance at "solo" sites was lower than that in *T. radiata* webs, one might argue that "solo" uloborids show less site tenacity because they move more often in search of good sites. However, there is no reason to suspect that the density of possible prey for "associated" spiders is greater than for "solo" ones, since both "associated" and "solo" spiders are found in similar tree buttresses. Thus, if disappearance from a site was only a function of prey density then "associated" and "solo" spiders would not be expected to differ in site tenacity. The fact that "associated" uloborids persisted longer at a site suggests that prey capture is easier in the host web for reasons mentioned below, or that mortality is higher outside of the host web, or both.

Greater site tenacity of "associated" uloborids is best explained by an increased rate of food capture that they enjoy in the host web. The size difference between "solo" and "associated" *P. vicina* suggests a difference in prey capture, though without being able to identify specific instars in the field, the finding that "associated" *P. vicina* are larger than "solo" ones is ambiguous. If larger instars were more successful in colonizing tengellid webs, then the difference in size would not necessarily be the result of greater prey capture. In the choice experiment, however, small spiders found the tengellid webs as well as medium or large uloborids. Results also showed prey capture to be significantly higher for "associated" uloborids. Unless it could be shown that larger spiders captured prey more frequently, the prey-capture data support the hypothesis that tengellid webs provide an increased probability of prey capture for *P. vicina.*

Increased prey capture of "associated" spiders may be due to the additional threads provided by the tengellid or to the increased density of uloborid frame lines inside the confinements of the host web, or both. The anomaly of figure 3, a positive correlation for "associated" uloborids but an insignificant correlation for "solo" ones, may be explained in terms of spider density at a particular site. By inhabiting the confines of a tengellid web, uloborids tend to be packed closer together, both vertically and horizontally, than they would be in a "solo" aggregation. An insect flying into the frame lines of one *P. vicina* may be thrown into the web of a conspecific if the webs are closely packed. "Solo" *P. vicina* tend to build primarily on a horizontal plane in relation to one another, placing their webs farther apart than uloborids within a tengellid web, thus decreasing their density relative to "associated" conspecifics.

An additional factor which may contribute to greater site tenacity found in "associated" *P. vicina* is the protection tengellid webs offer from predators and the elements. *Tengella radiata* webs are most often found hanging in the space between tree buttresses, hollow-out logs, or root masses. In such locations, uloborids would enjoy considerable protection from heavy, flightless predators such as frogs, or lizards, since such predators could reach the suspended spiders only by jumping onto the platform web which would break under their weight. In addition tengellid webs in buttresses offer protection from all but the heaviest rains. Only those "solo" *P. vicina* which build webs in the innermost recesses of tree buttresses, or in particularly well-sheltered sites (such as hollow, fallen trees), maintain their webs intact at the end of an afternoon rain (personal observation). A "rained-out" spider not only has fewer hours in which to capture prey, but it must exert additional energy in rebuilding the web, and runs a greater risk of predation during the time it is without a web.

Two further advantages of the association to *P. vicina* remain untested. Web-building time for uloborids inhabiting tengellid webs may be less than for "solo" ones. Buskirk (1975) found that colonial individuals of the orb weaver *Metabus gravis* took significantly less time to construct webs than did single *M. gravis*, because colonial spiders could utilize common frame lines. Uloborids do not take down a complete web at night if only a small portion needs repair. As mentioned earlier, "associated" webs are less susceptible to damage by rain, wind, and falling branches because of their position in a buttress. The probability is thus high that several frame lines would remain intact at the end of the day and may be reused. In addition, the webs of *T. radiata* may provide protection from uloborid egg parasites. Bradoo (1972) reports that the sticky web of *Stegodyphus sarasinorum*, the host of the commensal spider *Uloborus terokus*, protects the uloborid cocoons against egg parasites.

The association of *P. vicina* with *T. radiata* appears to be a commensal one. Because of the great difference in prey size and activity times of the two species, no interference in the activities of the other is apparent. I was unable to check for possible predation by *P. vicina* on newly emerged tengellid young since the tengellids were only beginning to oviposit when the study was terminated.

Philoponella vicina is unlike many other commensal spiders in that it catches prey independently of the host. Opell (1979) reports on a similar case of *P. tingena* which builds its web within webs of *Achaearanea.* Most of the commensal spiders so far identified in the literature feed on smaller prey caught in the host web, or on the remains of the host's meal (Exline 1945, Bristowe 1949, Vollrath 1979). Struhsaker (1969) found the uloborid *P. tingena* in the web of *Nephila clavipes*, but these did not build their own webs. Theridiid web parasites and occasional theridiosomatids and linyphiids were also found on the tengellid webs in my study, but none of these spiders built webs there.

This study focused on the "guest" half of the association, since it was more difficult to envision and test possible selective advantages for the tengellid host. One possible advantage for *T. radiata* is the deterrence *P. vicina* may provide from egg case parasitoids. Such parasitoids are known for spiders (Kaston 1948, Bradoo 1972) and tend to be small wasps which could get entangled in the uloborid webs. *P. vicina* may also benefit its host by preying upon the mites which were frequently observed on the tengellid's prey. Future work on this association should focus on "associated" and "solo" *T. radiata.* It may be that what I assume is a commensal relationship is, in fact, a mutualistic one.

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LITERATURE CITED

BRADOO, B. L. 1972. Life history and bionomics of *Idris* sp. (Scelionidae: Hymenoptera), egg parasite of *Uloborus*, a commensal on the web of social spider *Stegodyphus sarasinorum* (Karsch). Zool. anz. 188: 43-52.

———. 1979. *Uloborus ferokus* sp. nov. (Araneae: Uloboridae) a commensal of *Stegodyphus sarasinorum* Koch. Bull. Brit. arach. Soc. 4(8): 353-355.

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

BURGESS, J. W. 1976. Social spiders. Scient. Am. 234: 101-106.

———. 1979. Web signal processing for tolerance and group predation in the social spider *Mallos gregalis* Simon. Anim. Behav. 27: 157-164.

BUSKIRK, R. 1975. Coloniality, activity patterns, and feeding in a tropical orb-weaving spider. Ecology 56(6): 1314-1328.

———. 1981. Sociality in the Arachnida. *In*, H. R. Hermann. (Ed.). Social Insects Vol. II, Chap. 7. Academic Press.

CODDINGTON, J., AND O. FINCKE. 1979. Cohabitation in spiders. Organization for Tropical Studies, class book 79.1.

DARCHEN, N. R. 1965. Ethologie d'une araignée sociale, *Agelena consociata* Denis. Biol. Gabonica 1: 117-146.

DENIS, J. 1965. Un theridiide social du Gabon (Araneae: Theridiidae). Biol. Gabonica 1: 395-399.

EBERHARD, W. G. 1971. The ecology of the web of *Uloborus diversus* (Araneae: Uloboridae). Oecologia 6: 328-342.

ENDERS, F. 1975. Effects of prey capture, web destruction and habitat physiognomy on web site tenacity of *Argiope* spiders. J. Arachnol. 3(2): 75-82.

EXLINE, H. 1945. Spiders of the genus *Conopistha* from northeastern Peru and Ecuador. Ann. ent. Soc. Am. 38: 505-528.

HOLDRIDGE, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.

JACKSON, C. C., AND K. J. JOSEPH. 1973. Life history, bionomics and behavior of the social spider *Stegodyphus sarasinorum* Karsch. Insect. Soc. 20: 189-204.

KASTON, B. J. 1948. Spiders of Connecticut. Hartford, Conn. Geol. Nat. Hist. Surv. Bull. 70. 374 pp.

———. 1965. Some little known aspects of spider behavior. Am. Midl. Nat. 73: 336-356.

KULLMANN, E. J. 1972. Evolution of social behavior in spiders Araneae: (Eresidae and Theridiidae). Am. Zool. 12: 419-426.

KRAFFT, B. 1975. Les interactions limitant le cannibalisme chez les araignées solitaires et sociales. Bull. Soc. zool. Fr. 100: 203-221.

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

MUMA, M. H., AND W. J. GERTSCH. 1964. The spider family Uloboridae in North America north of Mexico. Am. Mus. Novit. 2196: 1-43.

OPELL, B. D. 1979. Revision of the genera and tropical American species of the spider family Uloboridae. Bull. Mus. comp. Zool. 148(10): 443-549.

PAIN, J. 1964. Premières observations sur une espèce nouvelle d'araignée sociale (*Agelena consociata* Denis). Biol. Gabonica 1: 47-58.

PETERS, H. M. 1953. Beträge zur vergleichenden Ethologie und Ökologie tropischer Webspinnen. Zeits. Morph. Ökol. Tiere 42: 278-306.

SIMON, E. 1981. Observations biologiques sur les Arachnides. I. Araignées sociables. Ann. Soc. ent. Fr. 60:5-14.

STRUHSAKER, T. T. 1969. Notes on the spiders *Uloborus mundior* (Chamberlin and Ivie) and *Nephila clavipes* (Linnaeus) in Panama. Am. Midl. Nat. 82(2): 611-613.

TIETJEN, W. J. 1977. Dragline following by male lycosid spiders. Psyche 84: 165-178.

TURNBULL, A. L. 1964. The search for prey by a web-building spider *Achaearanea tepidariorum* (C. L. Koch) (Araneae, Theridiidae). Canad. Ent. 96: 568-579.

VOLLRATH, F. 1979. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). Anim. Behav. 27: 515-521.