

**PREDATION BY A COMMENSAL SPIDER,
ARGYRODES TRIGONUM, UPON ITS HOST:
AN EXPERIMENTAL STUDY**

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ABSTRACT

Although the theridiid spider *Argyroides trigonum* has been described as a commensal, it has been found eating its host. In central Maryland *A. trigonum* often inhabits the web of the labyrinth spider, *Metepeira labyrinthea*. I performed a field experiment to assess the possible impact of *A. trigonum* upon labyrinth spider populations. Replicated groups of *M. labyrinthea* were established on four open experimental units in the species' natural habitat. Each unit was a wood frame supporting wire fencing on which the spiders built their webs. Mature *A. trigonum* females were added to two of the units and numbers of the labyrinth spider were monitored for 18 days. Numbers of *M. labyrinthea* declined more rapidly on the units to which *A. trigonum* had been introduced. More dead labyrinth spiders were found in these populations, and indirect evidence suggests that losses from emigration may have been higher in the presence of *A. trigonum*. Labelling *A. trigonum* as a commensal is probably misleading.

INTRODUCTION

Spiders of the genus *Argyroides* (Theridiidae) often behave as commensals, inhabitants of other species' webs that consume prey apparently neglected or undetected by the host spider [Exline 1945, Archer 1946 (1947), Comstock 1948, Kaston 1948, 1978, Legendre 1960 (cited by Kaston 1965), Gertsch 1979]. However, some tropical *Argyroides* spp. steal prey which the host has caught and thus clearly are kleptoparasites [Wiehle 1928, 1931, Thomas 1953, Kullmann 1959 (all cited by Kaston 1965), Robinson and Olazarri 1971, Robinson and Robinson 1973, Vollrath 1979]. Furthermore, some temperate *Argyroides* spp. apparently prey upon their hosts. Exline (Exline and Levi 1962) has observed *A. fictilium* (Hentz) [= *Rhomphaea lacerta* (Walckenaer)] eating *Araneus*. *Argyroides fictilium* will attack and eat *Frontinella pyramitela* (Walckenaer) [Archer 1946 (1947)], and *Argyroides* spp. have been found consuming another linyphiid, the filmy dome spider, *Neriene radiata* (Walckenaer) (pers. obs.; J. Martyniuk, pers. comm.). Lamore (1958) observed the common *Argyroides trigonum* (Hentz) [= *Conopistha rufa* (Walckenaer)] feeding upon a host basilica spider, *Mecynogea lemniscata* (Walckenaer). On several occasions my research assistants and I have found *A. trigonum* either feeding upon a basilica spider or in the web with the dead host. We have also observed *A. trigonum* eating the labyrinth spider, *Metepeira labyrinthea* Hentz.

I identified spiders as *A. trigonum* because of their similarity in size, color, and shape of the abdomen and egg sac, to the descriptions of this species given by Kaston (1948, 1978) and Exline and Levi (1962). Many *Argyrodes* that were found eating other spiders were not removed for a detailed examination because they were in the web of a host which was part of another ongoing field experiment. *A. cancellatus* (Hentz) is the only species with which *A. trigonum* occasionally may have been confused, particularly as juveniles. Most, if not all, spiders were probably correctly identified as *A. trigonum*. *A. cancellatus* may not be abundant in Maryland, since Kaston (1948) reports that it is quite rare in the north, but is common in Alabama. Also, Muma (1945) states that in Maryland *A. trigonum* occurs more often than *A. cancellatus* in the webs of *M. labyrinthea*.

In some instances *A. trigonum* may have been feeding upon a host which had died from other causes. However, the frequency with which I have observed *A. trigonum*

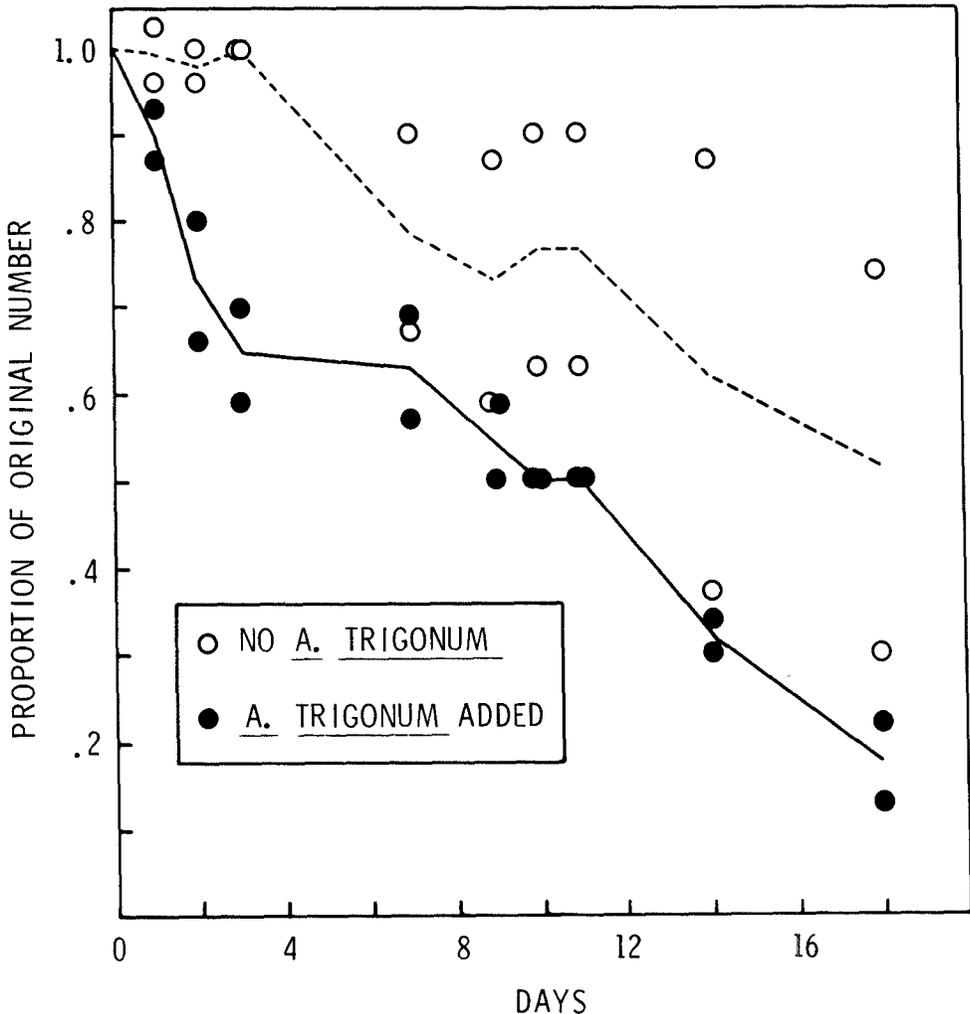


Fig. 1.—Effect of *A. trigonum* on numbers of *M. labyrinthea*. Population size of the labyrinth spider on each unit is expressed as the proportion of the number present on Day 0 (June 30). Numbers on all four units were similar at the beginning of the experiment. Initial population sizes on the control units were 27 and 31. On the units with *A. trigonum*, initial numbers of *M. labyrinthea* were 30 and 32.

eating other spider species suggests that it may regularly prey upon its host. To test this hypothesis I performed a field experiment to assess the potential impact of *A. trigonum* upon populations of *M. labyrinthea*.

METHODS AND MATERIALS

I conducted the experiment in mixed deciduous-pine woods on the Patuxent Wildlife Research Center, Prince Georges County, Maryland, U.S.A. This forest supports an abundant population of *M. labyrinthea* and has been the site of previous field experiments with this species (Wise 1979, 1981). Although labyrinth spiders spin webs on a variety of vegetation, for purposes of standardization the experiment was conducted with spiders that had spun webs on supports made of 5.1 cm mesh galvanized wire fencing (chicken wire) attached to wooden frames 4 m long, 2 m high, and 1.6 m wide. The wire was arranged in an undulating pattern that ran the length of each unit. Two rows of 2 waves, each 1 m high, were separated by a 1.6 x 4 m horizontal piece of fencing, and a similar piece was also secured to the unit's top. Four such structures ca. 10 m apart were used in the experiment. Units were not enclosed; thus no barriers prevented emigration and immigration of *M. labyrinthea*, their prey or their natural enemies.

During the last week of June 1980, immature male and female labyrinth spiders were collected from the surrounding woods and added at random to empty experimental units. By 30 June 60% had constructed webs on the wire. Mature female *A. trigonum* with egg cases were collected from another site and on 30 June were added to two randomly selected units. I taped each *A. trigonum*'s egg sac to the wire and then carefully placed the spider on her sac. Two units each received seven *A. trigonum* females, spaced evenly throughout the top half of each structure and as far as possible from occupied *M. labyrinthea* webs. Within two days most *A. trigonum* had detached the egg sac from the tape and had moved it to a newly constructed web 5-20 cm away from the point of introduction. No *A. trigonum* were added to the other two units, which served as controls. Neither *M. labyrinthea* nor *A. trigonum* individuals were marked. At the start of the experiment the numbers of *M. labyrinthea* in each population were: 27, 31 (control units) and 30, 32 (experimental units). Control and experimental populations were censused ten times from 30 June through 18 July. Three *A. trigonum*, one of which was a male, colonized the controls. These immigrants were removed and were added to the units to which *A. trigonum* had been intentionally introduced.

RESULTS AND DISCUSSION

On 1 July, 12 of the 14 *A. trigonum* which had been added the previous day were either in their own web with an egg sac (8) or in the web of a labyrinth spider (4). After one week 11 *A. trigonum* were on the units, two in webs of *M. labyrinthea*. A week later eight were present, of which six occupied *M. labyrinthea* webs. By 18 July the number of *A. trigonum* dropped to three and I ended the experiment.

The number of *M. labyrinthea* on the two units with *A. trigonum* declined rapidly during the first three days of the experiment, while numbers on the control units remained stable (Fig. 1). On the third day the proportion of labyrinth spiders remaining in the two populations with *A. trigonum* was significantly lower than in the control populations [$t=11.1$, $p < 0.01$; calculated from arcsin of the square root of the proportion, since proportions tend to be binomially distributed (Snedecor 1956)]. Between the third and

seventh day numbers in one control group declined suddenly: Nine of 27 spiders disappeared from this unit, whereas only 3 of 31 disappeared from the other control. During this period an *Argyrodes* female colonized the first control unit and was found in a previously occupied labyrinth web on 7 July. It is questionable whether a single *A. trigonum* would cause so many host spiders to vanish, though it may have invaded several webs before it was discovered. For the next few days numbers of labyrinth spiders on the control units were again relatively stable. For the remainder of the experiment the average number of labyrinth spiders in the experimental populations was lower than in the controls, though differences were no longer statistically significant as judged by t-tests. Plotting numbers on an arithmetic axis (as in Fig. 1), rather than logarithmic, reveals the magnitude of the initial drop in numbers, but makes it difficult to compare rates of population decline for the remainder of the study. The final number of *M. labyrinthea* on both experimental units, expressed as a proportion of the total number on the seventh day, was 0.28 (11/39). In the pooled control populations the proportion present at the end of the study was 0.67 (31/40). This difference suggests that *A. trigonum* was also affecting *M. labyrinthea* during the last half of the experiment; however, a statistical test was not employed since there was no *a priori* reason for calculating survival from the numbers present after a week.

Since the units were unenclosed, the more rapid decline of *M. labyrinthea* in the experimental populations could have resulted solely from increased emigration in response to web invasions by *A. trigonum*. However, evidence indicates that predation by the commensal spiders contributed to the greater losses from the experimental populations: On two occasions *A. trigonum* was observed eating its host, and twice *A. trigonum* was discovered in a web with a dead labyrinth spider. The overall documented mortality rate of *M. labyrinthea* was higher in the presence of *A. trigonum*. During the study 11 dead labyrinth spiders were found in their webs on the units to which *A. trigonum* had been added. Five of these spiders died during the first three days of the experiment. Only one dead spider was found among the control groups. The proportion of the decline in numbers during the experiment which was due to known deaths was 0.22 for the pooled experimental populations (11/51) and 0.04 for the combined control groups (1/27). This difference is statistically significant ($p = 0.03$, exact probability for the 2x2 contingency table). The decline in numbers for each treatment group, i.e. the net loss during the experiment, represents known mortality plus the net effects of immigration, emigration and undetected mortality. Some mortality in both populations may have resulted from other predators, such as the pirate spider, *Mimetus puritanus* Chamberlin. This specialized predator on other spiders occurred on control and experimental units during the experiment, and we have observed it preying upon *M. labyrinthea* at other times.

Subtracting known mortality from the total decline in numbers yields the apparent net emigration, which includes undetected mortality. In order to compare control and experimental treatments, an apparent net emigration rate was calculated by expressing the number of apparent emigrants as a proportion of the total initial number after subtracting the number of known deaths. For example, the rate for the two pooled experimental populations was $(51-11)/(62-11) = 0.78$. Since some of this loss may have resulted from predators that remove their prey from the webs, comparing emigration rates calculated in this manner implicitly assumes that undetected mortality from sources other than *A. trigonum* was similar for all populations of *M. labyrinthea*. This assumption is also the basis for pooling replicates in order to calculate an overall emigration rate for the entire experiment. The apparent net emigration rate of the labyrinth spider was significantly higher on the units to which *A. trigonum* had been added (0.78 versus 0.46;

$\chi^2 = 12.2$, $p < 0.001$, 2×2 contingency table), which suggests that some *M. labyrinthea* abandoned their webs in response to invasions by *A. trigonum*. Confirmation of this interpretation would require experimentation with marked labyrinth spiders on a larger number of experimental units.

The initial rapid drop in numbers in the populations with *A. trigonum*, the greater number of dead spiders in these populations, and the observations of *A. trigonum* eating *M. labyrinthea* constitute evidence that the former species may be a significant mortality factor in the dynamics of labyrinth spider populations. An accurate assessment of the impact of *A. trigonum* upon its host populations will require further experiments. In particular, future studies should incorporate different life stages of both species as well as greater numbers of replicated populations.

Describing *Argyrodes* spp. as commensals implies that they do not lower the fitness of their hosts. Accumulating evidence indicates that the relationship between *Argyrodes* spp. and their hosts is not always a benign commensalism. Although tropical *Argyrodes* species do capture small prey which apparently go unnoticed by the host, they also steal larger insects which the host has captured and wrapped. Several investigators have suggested that such kleptoparasitic behavior has a negative impact upon the host by causing it to move its web if the rate of prey stealing is too high (Robinson and Olazarri 1971, Robinson and Robinson 1976, Vollrath 1979). Rypstra (1981) has established a quantitative relationship between number of *Argyrodes* in the host's web, number of prey stolen, and tendency of the host, *Nephila clavipes* (L.), to abandon its web site. Energy requirements of constructing a new web and increased exposure to predation may lower the fitness of a spider which has vacated an otherwise suitable web in response to high rates of kleptoparasitism.

No quantitative estimates exist on the effect of temperate *Argyrodes* spp. on the prey capture rates of their hosts. Perhaps the potentially competitive interactions between temperate *Argyrodes* spp. and their hosts are often more commensal than kleptoparasitic. However, generally describing such web-sharing spiders as commensals is incorrect, since the significant impact of *A. trigonum* upon the *M. labyrinthea* populations in this experiment suggests that the few reports of predation by temperate *Argyrodes* spp. actually reflect relatively frequent behavior. Trail [1980 (1981)] has found that *A. baboquivari* is a conspicuous predator on the uloborid *Philoponella oweni* in the Chiricahua Mountains of Arizona, consuming eggs, hatchlings and adults. Most evidence of predation by *Argyrodes* spp. upon their hosts comes from temperate associations, though Lubin (1974) has discovered tropical *Argyrodes* kleptoparasites eating the eggs and recently emerged spiderlings of *Cyrtophora moluccensis*. Perhaps tropical kleptoparasites prey upon host species that are smaller than the conspicuous *Nephila* and *Argiope* spp. which have been studied extensively. Further examination of tropical *Argyrodes* associations should reveal whether this apparent behavioral difference is real. Valuable information would also be gained from further research on associations in temperate habitats. In particular, what is the role of factors such as host feeding rate, number of *Argyrodes* per web, and the relative size of host and *Argyrodes* in determining whether a particular interaction between *Argyrodes* and its host is commensal, kleptoparasitic or predatory? The nature of the interaction may vary as a function of such variables.

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