

FORAGING VERSATILITY AND THE INFLUENCE OF HOST AVAILABILITY IN *ARGYRODES TRIGONUM* (ARANEAE, THERIDIIDAE)

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ABSTRACT. *Argyroides trigonum* (Hentz 1850) can interact with its host as kleptoparasite, host predator, web-stealer, or commensal. This species can also capture insect prey in a web of its own construction. Which foraging strategy an individual *A. trigonum* exhibits certainly depends on a multitude of environmental factors, especially host availability. In this study, field surveys of populations of *A. trigonum* and its hosts and daily observations of individually marked host webs were made at sites in Ohio and New Hampshire. These observations together with a manipulation of *A. trigonum* density were performed in order to determine the influence of host species and abundance on the foraging strategy of *A. trigonum*. *A. trigonum* utilized *Neriene radiata* (Walckenaer 1841) to a greater extent than alternative hosts at both web sites even though many other host species were more abundant. The percentage of *A. trigonum* sharing a web with the host did not change with differing host/*A. trigonum* ratios; however, as a host/*A. trigonum* ratio increased, more *A. trigonum* were found in unoccupied host webs and fewer *A. trigonum* were found in webs of their own construction. *A. trigonum* is more likely to share a web with *Pityohyphantes costatus* (Hentz 1850) and to usurp the webs of *Neriene radiata*. Overall, *A. trigonum* behaved predominantly as a host predator; however, kleptoparasitism is more likely in host webs that last longer. Capturing prey in self-constructed or empty host webs is also important to *A. trigonum* foraging.

While some species utilize only one or a narrow set of behaviors to accomplish a certain task such as acquiring food, others exhibit a broad repertoire of behavioral strategies to achieve the same goal. Such behavioral versatility in a population could be the result of phenotypic plasticity of individuals responding to a variety of environmental pressures, genetic differences among individuals within a population, or both. Although some species of spiders are known to be quite versatile in their behavior (Jackson & Hallas 1986; Jackson & Poulsen 1990), very little research has been done to determine the correspondence between alternative behavioral strategies and their possible associated environmental factors.

The spider genus *Argyroides* Simon 1864 (family Theridiidae) is commonly thought to be comprised of species that forage primarily by invading the webs of other host spiders and kleptoparasitizing their captured prey, or behaving as commensals in host webs. However, some species have also been shown to be predators of their hosts (Exline & Levi 1962;

Smith-Trail 1980; Wise 1982; Tanaka 1984; Larcher & Wise 1985; Whitehouse 1986; Suter et al. 1989). According to Whitehouse (1986, 1987), those species that appear to be exclusively araneophages (or host predators) are members of the sub-genera *Rhomphaea* (L. Koch 1872) or *Ariamnes* (Thorell 1870), which may actually be genera distinct from *Argyroides* (although closely related). In fact, many species of *Argyroides* are both kleptoparasitic and araneophagic (Whitehouse 1986), and the foraging behavior of few species has been studied in enough detail to determine the full range of their foraging possibilities (but see Vollrath 1979a, b: *A. elevatus* Taczanowski 1873; Whitehouse 1986, 1988, 1993; *A. antipodiana* Cambridge 1880; and Cangialosi 1990, 1991: *A. ululans* Cambridge 1880). Work by Larcher & Wise (1985) and Cangialosi (unpubl. data) indicates that *Argyroides trigonum* (Hentz) utilizes an array of foraging tactics including kleptoparasitizing prey from a host web, using an occupied or unoccupied host web to capture its own prey, preying on the host spider, and cap-

turing insect prey in a web of its own construction. Elucidating the factors responsible for foraging versatility in *A. trigonum* should further our understanding of the ways in which the environment may or may not influence behavior.

Although many factors are probably influential in determining which foraging strategy is exhibited by an individual *A. trigonum*, the availability of hosts is presumably one of the most important. The major objectives of this investigation were to determine the diversity of host species utilized by *A. trigonum*, the relative importance of each of the different foraging modes it exhibits, and how foraging mode is influenced by host species and host abundance. In particular, I hypothesize that 1) changes in host abundance cause shifts in the percentages of *A. trigonum* exhibiting different foraging strategies, and 2) *A. trigonum* uses different foraging tactics when interacting with the host species, *Neriene radiata* Walckenaer (family Linyphiidae) than it does when interacting with the host species, *Pityohyphantes costatus* Hentz (family Linyphiidae). These two host species were selected for comparison because both are major hosts for *A. trigonum*, and differences between them in web structure and body size was expected to provide different foraging challenges for *A. trigonum*.

METHODS

Study sites.—Two study sites were used for data collection and comparison. One site was the forested portion of Miami University's Ecological Research Center in Oxford (Butler County), Ohio. The other was the Greater Goose Pond Forest in Keene (Cheshire County), New Hampshire. Both of these sites are temperate deciduous forest although the Keene site has a greater proportion of coniferous trees, especially white pine and hemlock. *Argyodes trigonum* and its hosts are common in the understory of both forests.

Study species.—*Argyodes trigonum* is common throughout the eastern portions of Canada (Ontario), and the United States from central Wisconsin to eastern Texas, and Maine to Florida (Exline & Levi 1962). The body length of adults ranges from approximately 2–4 mm. When not in a host web, *A. trigonum* builds a very small tangle web or hangs from just a few strands of silk. The two host species

used in the individual web observations, *Neriene radiata* and *Pityohyphantes costatus*, are both linyphiids. *Neriene radiata* builds a dome-shaped sheet web with barrier silk extending above the dome. The spider usually sits just beneath the central area of the dome. *Pityohyphantes costatus* builds a hammock-shaped triangular sheet which is flatter and longer than that of *N. radiata*. Barrier silk also extends above the sheet of *P. costatus*. *Pityohyphantes costatus* builds a retreat which usually consists of dense silk placed in a rolled leaf or under a piece of tree bark at one end of the sheet. The spider is often found within this retreat, or underneath the central part of its sheet web.

Ohio site field survey.—To gain some measure of overall host use by *A. trigonum* in this study site, a 20 × 2 m plot of forest was censused weekly from August–October 1990 for a total of 11 weeks. The number of web-building spiders of all species (if easily identified) or family present was recorded. I also recorded the presence of *A. trigonum* in a web with a host, in a host web alone, or in a web of its own construction. Then, the number of host spiders relative to the number of *A. trigonum* (host/*A. trigonum* ratio) was calculated for each date. The percentage of *A. trigonum* observed in each of the three above situations was plotted against host/*A. trigonum* ratio for all 11 dates and Spearman Correlation Coefficients were calculated.

New Hampshire site host/*Argyodes* ratio manipulation.—In the forests of New Hampshire, it is common to find short walls of piled stones (mostly granite) that were used as property dividers 100 or more years ago. Many understory spiders build webs on these rocks and the vegetation that grows between and around the rocks. I utilized one of these walls as a convenient way to define control and manipulated areas. The wall used was approximately 0.75 m high. Three areas along the wall, each 10 m in length and 1.5 m in width, were marked at the edges with painted tent stakes and randomly designated as control, removal or addition. The three areas were separated by approximately 40–50 m of stone wall that was ignored in this study. In order to create a wide range of host/*Argyodes* ratios, I manipulated *A. trigonum* density in two of the three areas. I removed all *A. trigonum* from the removal area beginning on 13 July

Table 1.—*Argyrodes trigonum* utilization of host webs at the New Hampshire and Ohio study sites. "With *A. trigonum*" indicates web sharing. (arg = *A. trigonum*). Data are from the control area of the NH site density manipulation and the Ohio site field survey.

Host spider	New Hampshire				Ohio			
	# of hosts alone	# with <i>A. trigonum</i>	% occupied webs with arg	# arg in host web alone	# of hosts alone	# with <i>A. trigonum</i>	% occupied webs with arg	# arg in host web alone
Linyphiidae								
<i>Neriene radiata</i>	471	16	3.3	44	277	30	9.8	92
<i>Frontinella pyramitela</i>	—	—	—	—	190	5	2.6	13
<i>Pityohyphantes costatus</i>	70	1	1.4	2	34	1	2.8	2
Other Linyphiidae	192	0	0	0	—	—	—	—
Theridiidae	782	0	0	0	—	—	—	—
Agelenidae	297	1	0.34	0	11	4	26.7	2
Orb Weavers	62	0	0	2	341	0	0	0

1993 and continuing every 1–2 days until 10 October 1993. *A. trigonum* were added to vegetation in the center of the addition area, but not directly in host webs, and kept at the level of 10–15 total individuals (checked every 1–2 days) in this same time period. The *A. trigonum* used for additions were those taken from the removal area as well as some spiders collected approximately two km away from the experimental areas. The control area was left alone.

The foraging situation of *A. trigonum* (sharing a web with host, in host web alone, or in self constructed web) was recorded for all individuals within the three areas every 1–2 days. Number of hosts and *A. trigonum* were also recorded in each of the three areas and the host/*A. trigonum* ratio was calculated for each observation date. The number of *A. trigonum* in the removal area was not zero because of continuous immigration of *A. trigonum* into this area. Observation of their foraging situation was made just before removal. As with the Ohio data, the percentage of *A. trigonum* observed in each of the three above situations was plotted against weekly host/*A. trigonum* ratio and Spearman Correlation Coefficients were calculated. (Weekly, instead of daily, ratios were used in order to make more direct comparisons with the Ohio data. I used the ratio for the first day of the week that counts were recorded). Because a wider range of host/*A. trigonum* ratio was exhibited in these manipulated areas compared to the Ohio site, two sets of Spearman correlations were performed for the New Hamp-

shire data: one for host/*A. trigonum* ratios of less than 6:1 (for comparison with the Ohio data), and another for all ratios. Additionally, the data from the control area was compared to the Ohio site field survey in order to compare overall host species utilization between the two sites (Table 1).

Observations of individual host webs.—

At the New Hampshire site, occupied webs of *Neriene radiata* and *Pityohyphantes costatus* were located and the web site and webs were individually marked by placing flagging on vegetation near the web and a twist tie at one edge of the web at its attachment to the vegetation. No spiders were marked. Observations of groups of 23–25 host-only occupied webs of each species were initiated on 15 June, 19 July, 9 August, and 26 August 1994, making a total of 94 *P. costatus* and 95 *N. radiata* webs that were observed. Each web was observed every day until the complete disappearance of the web. The following data were recorded: host was alone in its web, *A. trigonum* was alone in the host web, the host and *A. trigonum* were together in the web, the web was empty (no spiders), the web was destroyed or gone. If an *A. trigonum* invaded a host web, emigrated, and then another (or the same) *A. trigonum* invaded that web later, the host web was considered to be invaded twice. Because several host webs were invaded by *A. trigonum* more than once, the total number of observations beginning with a host alone in its web was 148 for *P. costatus*, and 107 for *N. radiata*.

I initially summarized these observations

by constructing an ethogram of all fates of host webs with respect to the invasion of *A. trigonum*. Then, frequency of transition (%) from one state to the next was calculated between all states (i.e., host alone, *Argyrodes* alone, *Argyrodes* and host together, etc.) for both host species. These frequencies were compared between the two host species using contingency table analysis for the following: the frequency of web sharing and web takeover, the outcome of web sharing (the frequency of *A. trigonum* emigration and host emigration); and the outcome of web takeover (the frequency of host reclaiming the web and *A. trigonum* emigration). Mean duration of web sharing and web takeover were compared between the two host species using Kruskal-Wallis tests.

I also calculated the frequency of empty web invasion by *A. trigonum*, and compared the persistence (mean duration) of empty webs invaded and not invaded by *A. trigonum* between host species by log-transforming the non-normally distributed data and then utilizing a 2-way ANOVA. Additionally, mean duration of occupied host webs was compared between host species with a Kruskal-Wallis test.

RESULTS

Host utilization.—Data from the Ohio site field survey and the control area of the New Hampshire site density manipulation were used in Table 1 to compare overall host species/family utilization between these two sites. *A. trigonum* uses a variety of hosts; however, a preference for *Neriene radiata* was seen in both the New Hampshire and Ohio study sites. The percentage of *A. trigonum* observed sharing a web with *N. radiata* was 2–9× higher compared to most of the other hosts (Table 1). Also, the number of *A. trigonum* in empty webs (no host present) was 7–50× higher in the webs of *N. radiata* compared to the other host spiders. *A. trigonum* also made substantial use of *Frontinella pyramitela* (Walckenaer 1841)(family Linyphiidae) at the Ohio site, and *Pityohyphantes costatus* at both sites (Table 1). The number of agelenids in the study area at the Ohio site was only 11, but nearly a third of these were observed with an *A. trigonum* individual in their webs. Although there were several hundred agelenids, other linyphiids and theridiids observed at the New

Hampshire site, *A. trigonum* made little or no use of these hosts. Orb weavers were never observed sharing a web with *A. trigonum*, and only two empty orb webs contained an *A. trigonum* individual (Table 1).

Host abundance and foraging mode.—*A. trigonum* foraging mode was influenced by the relative number of hosts available in some cases in both the Ohio survey and the manipulation at the New Hampshire site. Due to the manipulation and the smaller area sizes, the range of host/*A. trigonum* ratios was much greater in the New Hampshire site (from 1.4:1 to 67:1 for New Hampshire, and all less than 5:1 in Ohio). There were no significant relationships between host/*A. trigonum* ratio and any of the three foraging situations at the New Hampshire site when the full range of ratios are included in the analyses. However, when host/*A. trigonum* ratios of less than 6:1 are considered, some patterns emerge that are similar to the Ohio site data.

At the Ohio site, the percentage of *A. trigonum* observed in a web of its own construction decreased significantly with an increase in the host/*A. trigonum* ratio (Spearman Coeff. $R = -0.644$, $P < 0.05$, Fig. 1a). This same pattern was seen at the New Hampshire site (Spearman Coeff. $R = -0.769$, $P < 0.001$, Fig. 1b). At the Ohio site, the percentage of *A. trigonum* observed in host webs alone increased significantly with an increase in the host/*A. trigonum* ratio (Spearman Coeff. $R = 0.725$, $P < 0.01$, Fig. 1c). However, this relationship was not seen at the New Hampshire site (Spearman Coeff. $R = 0.449$, $P = 0.192$, Fig. 1d). There was no relationship between the percentage of *A. trigonum* sharing a web with a host spider and the host/*A. trigonum* ratio at either site (Ohio: Spearman Coeff. $R = -0.198$, $P > 0.10$, Fig. 1e; New Hampshire: Spearman Coeff. $R = 0.056$, $P > 0.5$, Fig. 1f).

Host species and foraging mode.—The observations of *N. radiata* and *P. costatus* webs at the New Hampshire site revealed several sequences that took place with respect to the invasion of *A. trigonum* from the time that a host was first observed occupying its web alone until that web's demise. These sequences are summarized as a whole in Fig. 2 and subsets of this figure appear in Figs. 3, 4. Overall, a high percentage of host webs were invaded by *A. trigonum*. Of the total number

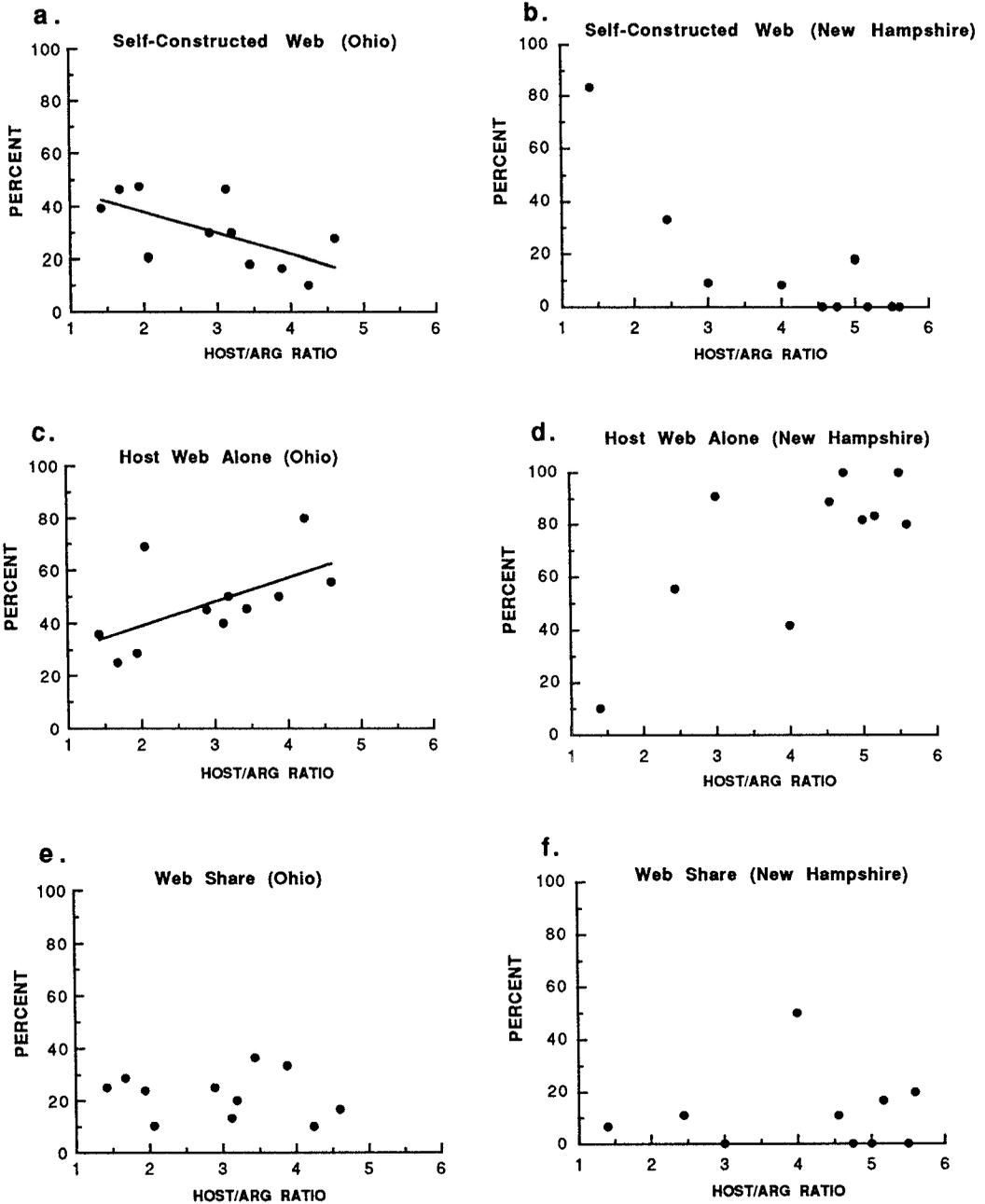


Figure 1.—Percentage of *Argyrodes trigonum* found in unoccupied host webs (host web alone), occupied host webs (web share), or in self-constructed webs, compared to relative host abundance for the Ohio survey (a, c, e) and the New Hampshire density manipulation (b, d, f). ARG = *Argyrodes trigonum*.

of observations beginning with a host alone in its web, 45.9% of *P. costatus* webs and 54.2% of *N. radiata* webs were invaded by *A. trigonum* (Fig. 3). There were 30 webs that were invaded more than once. For *P. costatus*,

17 webs were invaded twice, three webs were invaded three times, and one web was invaded four times. For *N. radiata*, seven webs were invaded twice and two webs were invaded three times.

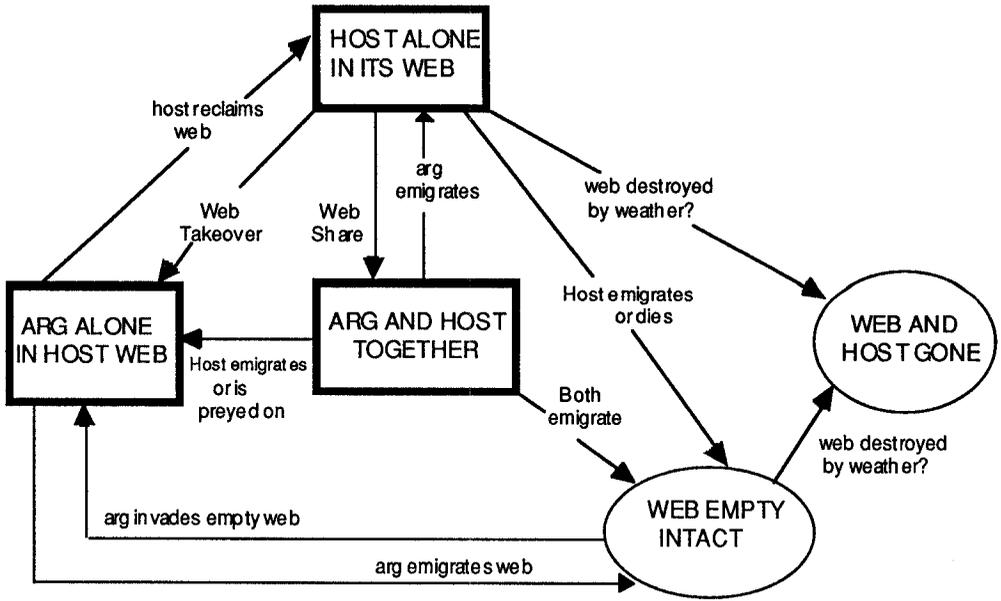


Figure 2.—Fates of host occupied, *Argyrodes trigonum* occupied, both occupied, and empty webs for individual webs observed at the New Hampshire site. (This figure can be compared to Figs. 3 & 4 to determine percentage outcome for observations beginning with the rectangular boxes.)

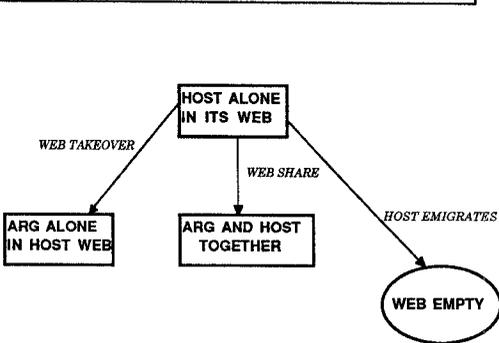
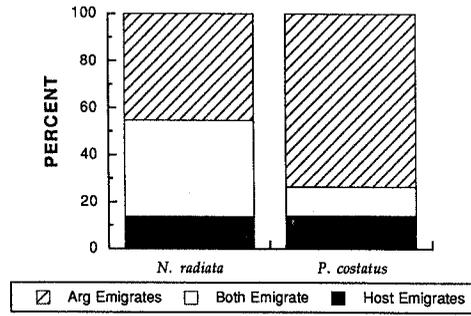
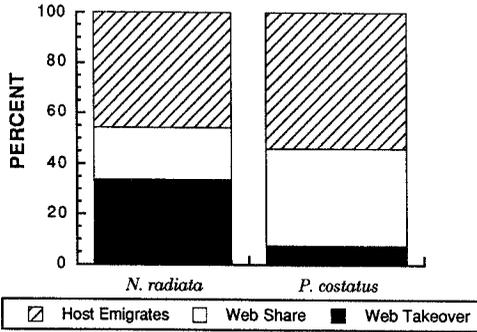


Figure 3.—The percentage of total host-only occupied webs that were either taken over by an *Argyrodes trigonum*, shared with an *Argyrodes trigonum*, or host emigrated/web destroyed for both *Neriene radiata* ($n = 107$) and *Pityohyphantes costatus* ($n = 148$) webs ($\chi^2 = 30.97, P < 0.0001$).

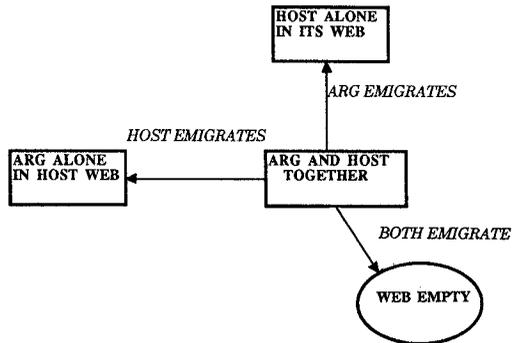


Figure 4.—Web sharing outcome. The percentage of host and *Argyrodes trigonum* occupied webs that resulted in *Argyrodes trigonum* emigration, host emigration, or both emigrating for both *Neriene radiata* ($n = 22$) and *Pityohyphantes costatus* ($n = 57$) webs ($\chi^2 = 7.73, P < 0.05$).

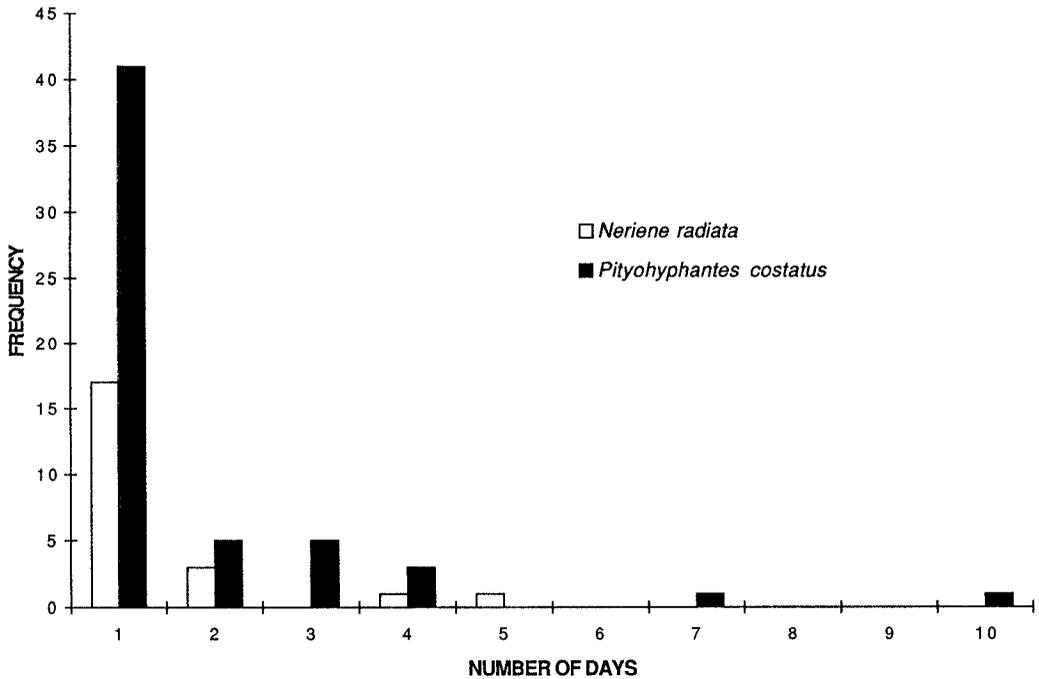


Figure 5.—Web sharing time. Frequency distribution of time (days) *Argyrodes trigonum* spent in occupied host webs for both host species.

Web sharing vs. web takeover: In order for *A. trigonum* to eventually usurp a host's web, there must be some period of co-occupation of the web with that host. Web takeover here refers to an *A. trigonum* individual observed to be alone in a host web within 24 h of that web having been observed with the host as the sole occupant, while web sharing refers to the host and *A. trigonum* co-occupying the web for at least 24 h. The invasion of occupied host webs by *A. trigonum* more frequently resulted in web takeover for *N. radiata* and in web sharing for *P. costatus* ($\chi^2 = 30.97$, $P < 0.0001$, Figs. 2, 3). Web takeover may indicate either host predation or web stealing (through forced host emigration). Although webs generally were not observed for more than a few minutes on each day, I did observe direct evidence of host predation on several occasions. There were four observations of *N. radiata* being fed on by *A. trigonum*, or a dead *N. radiata* in the web next to an *A. trigonum*, and one observation of *A. trigonum* feeding on *P. costatus*. All of these webs had a hole torn in the dome or sheet approximately 2–4 cm in diameter. Most of the host webs that were seized by *A. trigonum* were observed

with large holes in the dome or sheet portion of the web. I also observed the host being chased off its web by *A. trigonum* a total of two times, once for each of the two host species. The reverse situation was observed once when an *A. trigonum* individual was chased off the host web by *P. costatus*.

Outcome and duration of web sharing: There was a significantly higher proportion of *A. trigonum* only emigrating from *P. costatus* webs, and a significantly higher proportion of both host and *A. trigonum* emigrating from *N. radiata* webs after a period of web sharing ($\chi^2 = 7.73$, $P < 0.05$, Figs. 2, 4). There was no difference between the two host species in the frequency of the host giving up the web and leaving *A. trigonum* alone after web sharing occurred. Also, mean duration of web sharing was not significantly different for *P. costatus* compared to *N. radiata* (Kruskal-Wallis: $\chi^2 = 0.195$, $P = 0.659$, Fig. 5). Whereas web sharing never lasted longer than five days for *N. radiata*, there were two observations of web sharing for *P. costatus* that continued for a greater period of time than this, one for seven days and one for 10 days (Fig. 5).

Outcome and duration of web takeover:

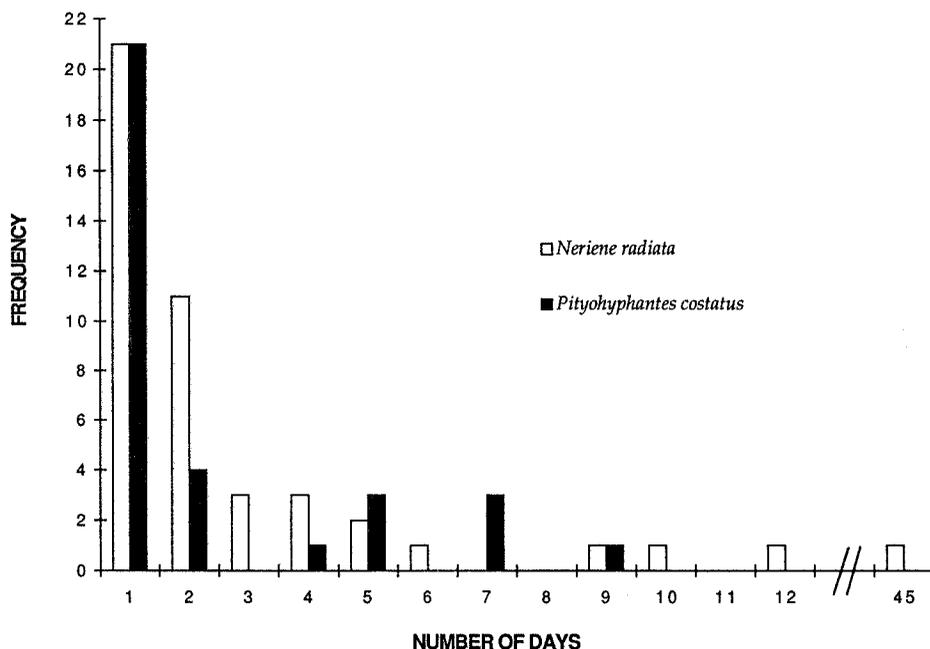


Figure 6.—Time alone in host web. Frequency distribution of time (days) *Argyrodes trigonum* spent in unoccupied host webs for both host species.

Once an *A. trigonum* had become sole occupant of a host web, the likelihood of a host regaining control of that web was small for both host species (less than 10% of webs). The percentage of webs reclaimed by host spiders after being usurped by *A. trigonum*, was not significantly different between *P. costatus* and *N. radiata* ($\chi^2 = 1.34$, $P > 0.24$). The mean duration of *A. trigonum* alone in a host web was not significantly different for the two types of host webs (Kruskal-Wallis: $\chi^2 = 1.17$, $P = 0.278$, Fig. 6). The longest periods of time that an *A. trigonum* spent alone in a host web were in *N. radiata* webs. There were three observations of an *A. trigonum* spending 10, 12, and 45 days alone in a *N. radiata* web (Fig. 6).

Table 2.—ANOVA for mean duration (log-transformed) of empty host webs invaded and not invaded by *Argyrodes trigonum*.

Source	df	Sum of squares	F-ratio	$P > F$
Host species	1	0.621	6.722	0.010
Invasion	1	1.665	18.023	<0.0001
Species \times invasion	1	0.030	0.326	0.568

Persistence of occupied and unoccupied webs.—The average time beginning with a host first observed in its web until the host was gone, was significantly greater for *P. costatus* (*P. costatus*: mean \pm SE = 9.74 \pm 1.15 days, $n = 70$; *N. radiata*: mean \pm SE = 3.74 \pm 0.63 days, $n = 46$; Kruskal-Wallis: $\chi^2 = 13.77$, $P < 0.001$). Host webs that became devoid of a host spider (empty) were sometimes invaded by *A. trigonum*. For *P. costatus*, 19.4% (18 out of 93) of empty webs were invaded by *A. trigonum* compared to 9.2% (8 out of 87) of empty *N. radiata* webs. The persistence of a web without its host spider was significantly longer for those webs that were invaded by *A. trigonum* compared to webs that were never invaded (Table 2). As with occupied webs, empty *P. costatus* webs lasted significantly longer than *N. radiata* webs (Table 2).

DISCUSSION

Vollrath (1984) classified species of *Argyrodes* as either generalists or specialists, where generalists are those species that utilize a wide variety of hosts from different families, and specialists are restricted to one or a few host species. Whitehouse (1988) added that

generalists use only a few techniques to obtain food, while specialists utilize several techniques. However, a host generalist might be expected to need a wider scope of foraging techniques in order to deal with hosts of differing size, defensive ability, and web type. *A. trigonum* appears to be a generalist in both senses as it uses a variety of hosts and a variety of foraging strategies.

Although *A. trigonum* utilized several types of hosts at both the Ohio and New Hampshire sites, its presence in the webs of hosts was not in proportion to the number of those hosts or host webs available. Even as a generalist, *A. trigonum* shows a preference for certain host types which were mainly linyphiids at these study sites. The eleven agelenid webs at the Ohio site were large (about 30 cm in diameter) and provided an extensive amount of barrier webbing which might explain the extremely high percentage of *A. trigonum* in their webs. The agelenids, theridiids, and other linyphiids at the New Hampshire site were mostly juveniles within the time period of this study, tended to have little barrier silk, and built their webs deep in the small spaces between the rocks. These characteristics likely made these hosts less accessible or functional to *A. trigonum*. Overall, the number of *A. trigonum* at the New Hampshire site was low compared to the Ohio site, especially considering that a greater number of webs at the New Hampshire site were surveyed. In this study, *A. trigonum* made virtually no use of orb weavers. At a site in Maryland, *A. trigonum* is found often in the webs of the orb weaver, *Metepeira labyrinthea* Hentz 1847 (family Araneidae) (Wise 1982; Larcher & Wise 1985). Orb weavers in this genus build a barrier web in addition to the orb whereas most others do not. I have never observed *M. labyrinthea* at the New Hampshire site, and have only seen a few individuals at the Ohio site in the course of several years. Although *A. trigonum* exhibits preferences for certain hosts when choices are available, its ability to utilize many different hosts may be largely responsible for its wide geographical distribution.

In this study, *A. trigonum* was observed occupying the web of a host that is no longer present, occupying the web of a host that is present (web sharing), and occupying a self-constructed web. Changes in relative host abundance influence *A. trigonum* foraging

mode to a certain extent by altering the percentage of *A. trigonum* found in these three situations. However, determining precisely how individuals shift their mode of foraging is difficult because these situations indicate a complexity of foraging alternatives (Table 3). Also, foraging is certainly influenced by a variety of other factors. The abundance data together with the observations of individual host webs reveals more about the relative extent to which *A. trigonum* behaves as a kleptoparasite, predator, web stealer, or independent forager.

Several pieces of evidence indicate that *A. trigonum* behaves as a spider predator or web stealer to a greater extent than a kleptoparasite in these two study areas. More *A. trigonum* were observed in unoccupied host webs than in occupied host webs at both the Ohio and New Hampshire sites. Also, there was a higher percentage of *A. trigonum* in unoccupied host webs than in either of the other two situations (in occupied host webs, in self-constructed webs) in all three of the areas in the manipulation (addition, removal, control). Because the percentage of total hosts at any one time with *A. trigonum* in their webs was fairly low (about 1–10%), and the percentage of observed webs that eventually were invaded by *A. trigonum* was high (45.9–54.2%), it seems that relatively few *A. trigonum* move around quite frequently and eventually invade a large portion of the available webs. This high mobility in general is more consistent with a predatory or web-stealing as opposed to a kleptoparasitic lifestyle. The direct observations of host predation support this claim as well.

In spite of the largely predatory nature of *A. trigonum*, the importance of prey kleptoparasitism cannot be ruled out. About 20% of *A. trigonum* both in the manipulation in New Hampshire and in the Ohio survey were consistently observed in an occupied host web (web sharing), regardless of host density. In comparing the two host species, web sharing occurred more frequently with *P. costatus* whereas web takeover was more likely with *N. radiata*. This is probably related to the fact that occupied *P. costatus* webs last longer than *N. radiata* webs and provide a greater amount of barrier silk. Host size (Larcher & Wise 1985) and defensive behavior are also important. *P. costatus* is somewhat larger and

Table 3.—Three major situations in which an *Argyrodes trigonum* individual can be found in relation to a host and the modes of foraging and access to foraging sites that these situations indicate.

<i>Argyrodes trigonum</i> /host web situation	<i>Argyrodes trigonum</i> foraging modes and access to foraging sites
Occupy host web alone	<ol style="list-style-type: none"> 1) has preyed on the host (host predator) 2) has caused the host to emigrate and is using the host web for insect prey capture (web stealer) 3) has invaded an empty host web and is using it for insect prey capture (web scavenger)
Share web with host	<ol style="list-style-type: none"> 1) is taking insect prey unimportant to the host (commensal) 2) is taking insect prey important to the host (kleptoparasite) 3) is in a temporary transition stage to steal host web or prey on the host
In self-constructed web	<ol style="list-style-type: none"> 1) is foraging for insect prey (independent forager) 2) is in the process of host web location

usually resides in a retreat at the edge of its web under bark or in a rolled leaf. This may explain why a greater percentage of *A. trigonum* emigrated from *P. costatus* webs compared to *N. radiata* webs leaving the host alone again after a period of sharing. Larcher & Wise (1985) also found that the probability and duration of web sharing was different for different host species. *Metepeira labyrinthea* were less likely to abandon their webs when invaded by *A. trigonum* compared to *N. radiata*, although *A. trigonum* did prey on *M. labyrinthea* at a substantial rate. In general, it seems reasonable to assume that in areas which are dominated by larger host species with long lasting webs and a large amount of barrier or tangle silk, and perhaps reside in retreats (e.g., large agelenids, theridiids such as *Achaearanea tepidariorum* C.L. Koch 1841), *A. trigonum* will behave predominately as kleptoparasites or commensals.

The significance of capture of their own insect prey by *Argyrodes* (whether by use of a host web or a self-constructed web) as a way of obtaining food, has been minimized or ignored by most workers. Vollrath (1984), in his review of kleptobiotic interactions in invertebrates, even states: "no *Argyrodes* is known to construct and operate a feeding web". However, Eberhard (1979) described in detail the use of a self-constructed web by *A. attenuatus* in order to capture prey which included not only spiders but a large proportion of insects. Although this web differs from the typ-

ical theridiid snare, it is used as a substrate for the capture of insect and spider prey and could therefore be considered a capture web. *A. antipodiana* will attack and subdue flies on both its own and the host's web (Whitehouse 1986). I have observed *A. trigonum* capture and feed on insects on a self-constructed web both in the laboratory and in the field (unpubl. obs.). Larcher & Wise (1985) showed that *A. trigonum* captured more than 50% of the insects that they introduced into host unoccupied webs. In this study, there was always at least 15%, and up to 40%, of the total population (at both sites) that were found in webs of their own construction.

Determining the occurrence of predation versus web-stealing may help clarify the importance of self prey capture (capturing its own insect prey) for *A. trigonum*. Once an *A. trigonum* had usurped a host's web, most emigrated from that web after 1–2 days. Because a web devoid of its host can last about 3–6 days, it appears that predation is usually the goal (whether or not the *A. trigonum* was successful). Nonetheless, 29% of *A. trigonum* in unoccupied *N. radiata* webs, and 24% of *A. trigonum* in unoccupied *P. costatus* webs, stayed for three days or longer with one individual remaining in the same *N. radiata* web for 45 days. Additionally, since empty webs that are invaded by *A. trigonum* last longer than those that are not, this implies that either *A. trigonum* is expending energy in maintenance and repair of the web, or staying in

those webs that happen to last longer. The individual that resided in the same web for 45 days definitely added silk and altered the web considerably so that it was no longer recognizable as a *N. radiata* web. One might view this as stealing the web site rather than just the web. In any case, using the host web for prey capture seems to be an important foraging mode for a substantial portion of the population. (One note of caution with this conclusion relates to the fact that the *A. trigonum* emigration frequency distribution in Fig. 6 follows an exponential decay function. Suter & Sanchez (1991) have presented strong evidence that such relationships may indicate a "rolling dice" criterion for decision making, especially if those organisms face an unpredictable environment. If this is true here, some individuals may just be randomly waiting longer before moving on to their next predation attempt). *Argyrodes* almost certainly evolved from web-building ancestors, and their current use of self prey capture may still represent a significant amount of their food intake for some species and therefore be more than just a evolutionary vestige.

Whitehouse's (1986) proposed models for the evolution of kleptoparasitism in *Argyrodes* imply that although both araneophagy and kleptoparasitism are present in most species, the foraging behavior of all ancestors and current species of *Argyrodes* is dominated by a single strategy. But these data show that there appears to be no consistent dominant foraging mode for *A. trigonum*, and which strategy it uses depends largely upon the abundance and species of hosts (or prey spiders) that are available. Other environmental factors such as insect availability probably influence *A. trigonum* foraging mode as well and should be investigated in the future.

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LITERATURE CITED

- Cangialosi, K.R. 1990. Social spider defense against kleptoparasitism. *Behav. Ecol. Sociobiol.*, 27:49-54.
- Cangialosi, K.R. 1991. Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. *Anim. Behav.*, 41:639-647.
- Eberhard, W.G. 1979. *Argyrodes attenuatus* (Theridiidae): A web that is not a snare. *Psyche*, 86: 407-413.
- Exline, H. & H.W. Levi. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). *Bull. Mus. Comp. Zool.*, 127:75-204.
- Jackson, R.R. & S.E.A. Hallas. 1986. Predatory versatility and intraspecific interactions of sparteine jumping spiders (Araneae: Salticidae): *Brettus adonis*, *B. cingulatus*, *Cyrbia algerina*, and *Phaeacius* sp. indet. *New Zealand J. Zool.*, 13:491-520.
- Jackson, R.R. & B.A. Poulsen. 1990. Predatory versatility and intraspecific interactions of *Suppuna picta* (Araneae: Clubionidae). *New Zealand J. Zool.*, 17:169-184.
- Larcher, S.R. & D.H. Wise. 1985. Experimental studies of the interactions between a web-invading spider and two host species. *J. Arachnol.*, 13:43-59.
- Smith-Trail, D. 1980. Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders. *Psyche*, 87:349-355.
- Suter, R.B. & E. Sanchez. 1991. Evolutionary stability of stochastic decision making in spiders: Results of a simulation. *Anim. Behav.*, 42:921-929.
- Suter, R.B., C.M. Shane & A.J. Hirscheimer. 1989. Spider vs. spider: *Frontinella pyramitela* detects *Argyrodes trigonum* via cuticular chemicals. *J. Arachnol.*, 17:237-240.
- Tanaka, K. 1984. Rate of predation by a kleptoparasitic spider, *Argyrodes fissifrons* upon a large host spider, *Agelena limbata*. *J. Arachnol.*, 12: 363-367.
- Vollrath, F. 1979a. Behavior of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). *Anim. Behav.*, 27:515-21.
- Vollrath, F. 1979b. Vibrations: Their signal function for a spider kleptoparasite. *Science*, 205: 1149-1151.
- Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. Pp. 61-94. *In* Producers and scroungers: Strategies of exploitation and parasitism. (C.J. Barnard, ed.). Grom Helm, London & Sydney.
- Whitehouse, M.E.A. 1986. The foraging behaviours of *Argyrodes antipodiana* (Theridiidae), a kleptoparasitic spider from New Zealand. *New Zealand J. Zool.*, 13:151-168.
- Whitehouse, M.E.A. 1987. "Spider eat spider": The predatory behavior of *Rhomphaea* sp. from New Zealand. *J. Arachnol.*, 15:355-362.
- Whitehouse, M.E.A. 1988. Factors influencing

- specificity and choice of host in *Argyrodes antipodiana* (Araneae, Theridiidae). *J. Arachnol.*, 16:349–355.
- Whitehouse, M.E.A. & R.R. Jackson. 1993. Group structure and time budgets of *Argyrodes antipodiana* (Araneae, Theridiidae), a kleptoparasitic spider from New Zealand. *New Zeal. J. Zool.*, 20:201–206.
- Wise, D.H. 1982. Predation by a commensal spider, *Argyrodes trigonum*, upon its host: An experimental study. *J. Arachnol.*, 10:11–16.
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