

***Argyroides fissifrons* Inhabiting Webs of *Cyrtophora* Hosts: Prey Size Distribution and Population Characteristics**

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I-Min Tso and Lucia Liu Severinghaus (2000) *Argyroides fissifrons* inhabiting webs of *Cyrtophora* hosts: prey size distribution and population characteristics. *Zoological Studies* 39(3): 236-242. In this field study we investigated the impact of *Argyroides fissifrons* (Araneae: Theridiidae) on two species of *Cyrtophora* spider hosts (Araneae: Araneidae) by studying several aspects of its population and foraging. We examined (1) if natural population variations of *A. fissifrons* occur with different web sizes of the hosts, (2) if *A. fissifrons* form long-term associations with particular hosts, and (3) if the size range of prey consumed by *A. fissifrons* overlaps with that of *Cyrtophora* hosts. Results from field surveys indicated that a positive relationship exists between the average number of *A. fissifrons* and the size of the host webs. The number of *A. fissifrons* per host web per day changed daily, indicating the daily occurrence of immigration-emigration events. However, as inferred from monitoring marked *A. fissifrons* for 3 nights, some individuals form a long-term association with a particular host. The sex ratio, body size, and prey intake of *A. fissifrons* spiders staying in particular hosts' webs during monitoring did not differ from those that left a web. A significant difference was found in prey size distribution between *Cyrtophora* hosts and *A. fissifrons*, and the average prey size of the former was far greater than that of the latter. This result suggests that *A. fissifrons* scavenge on webs of *Cyrtophora* hosts by collecting small prey ignored by the hosts.

Key words: *Argyroides*, *Cyrtophora*, Orchid Island, Spider.

A number of spiders are obligate users of webs spun by other spiders as habitats for resting, foraging, mating, and/or reproduction. Spider species from at least 19 families reported to inhabit webs spun by other species are either mutualistic, commensal, or detrimental to their hosts (Vollrath 1987, Elgar 1993 1994). Among numerous web inhabitants, theridiid spiders of the genus *Argyroides* have received the most documentation. Except for a few species which catch prey with their own webs (Eberhard 1979, Whitehouse and Jackson 1998), most *Argyroides* species inhabit webs of other spiders. The long appendages and highly sensitive vibration organs enable them to move stealthily in the web, effectively detect trapped prey, and accurately orient toward it (Vollrath 1979a, Foelix 1996). Depending on the relative sizes of the hosts (Larcher and Wise 1985), *Argyroides* is either commensal to the hosts by collecting tiny prey normally not taken by hosts (Exline and Levi 1962, Liao et al. 1984) or are

detrimental to the hosts by (1) stealing normal prey items from the host (Vollrath 1979b, Whitehouse 1988, Cangialosi 1991), (2) forcing the hosts to relocate webs more often (Rypstra 1981, Grostal and Walter 1997), (3) removing silk from the hosts' webs (Tso and Severinghaus 1998), or (4) preying upon the host (Smith Trail 1981, Tanaka 1984, Larcher and Wise 1985) or its eggs (Pasquet et al. 1997).

Recently, we found webs spun by solitary araneid spiders of the genus *Cyrtophora* on Orchid Island, Taiwan to be inhabited by a large *Argyroides* spider, *A. fissifrons*, and almost nothing is known about this association. *Cyrtophora*, a unique member of the orb-weaver family, constructs a huge modified orb web composed of a dome-shaped tangle barrier above a horizontal bowl web woven with a very fine mesh. All developmental stages of *A. fissifrons* are frequently seen on both the tangle threads and horizontal orb webs of *Cyrtophora* hosts. In some cases, as many as 20 *A. fissifrons*

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can be seen on 1 *Cyrtophora* web. Thus far, no one has studied the *A. fissifrons*-*Cyrtophora* association, and the potential impact of *A. fissifrons* on the hosts is not clear. To gain a basic understanding of the mode of association between them, we investigated the population characteristics and foraging behaviors of *A. fissifrons* by asking the following: (1) Will natural population variations of *A. fissifrons* occur with differences in web size of the hosts? (2) Will *A. fissifrons* form long-term associations with particular host webs? (3) Will foraging by *A. fissifrons* significantly affect that of the hosts?

MATERIALS AND METHODS

The study site

This study was conducted between March and May and between October and December 1997 on Orchid Island (*Lanyu* in Chinese, 22°N, 121.5°E), a tropical volcanic island 91 km off the southeast coast of Taiwan. During the study we visited Orchid Island once each month (6 trips in total), and each field trip lasted 5 d. Orchid Island's climate is characterized by high temperature (average 22.4 °C), high precipitation (more than 2600 mm per year), and thus high relative humidity (more than 90%). The study site (under Chung-Ai bridge) is in a dry river bed which stretches about 500 m, and winds through a tropical forest on the southwest end of the island.

Natural population variation of *A. fissifrons*

In this portion of the study we investigated whether or not natural variations in numbers of *A. fissifrons* correlated with size of the host webs. Webs built by *Cyrtophora* spiders are characterized by having a tangled scaffolding above a bowl web. We marked web sites of *Cyrtophora* hosts by fastening colored plastic strips to vegetation nearby. For each marked host web site we recorded the following variables: radius of the bowl (cm), height of the tangle scaffold (cm, measured from middle of the tangle) and body length of the host (mm). In addition, we also recorded numbers of *A. fissifrons* in the hosts' webs for 3 consecutive nights. To examine if larger hosts constructed larger webs, we performed linear regressions between host body length and (1) the height of the tangle and (2) the area of the bowl webs. To examine if larger host webs tended to be invaded by more *A. fissifrons*, we performed 2 more linear regressions between the number of inhabiting *A. fissifrons* and (1) the height of the tangle and (2)

the area of the bowl webs. Although the 2 species of *Cyrtophora* hosts differ in adult size, no significant difference was found when comparing body lengths of the 2 species of marked individuals (Mann-Whitney $U = 632.5$, $p > 0.05$), which may result from the incorporation of hosts of all developing stages in the study. Therefore, data collected from the 2 species of hosts were pooled in the analysis.

Tenacity of *A. fissifrons* in webs of *Cyrtophora* hosts

We examined the tenacity of *A. fissifrons* spiders to determine whether or not they form long-term association with the hosts, or whether they move frequently between host webs as described in many *Argyrodes*-host systems (Whitehouse and Jackson 1993, Tso and Severinghaus 1998). This question was approached in 2 ways. First, we examined whether the average numbers of *A. fissifrons* per host web per day recorded from April, May, October, and December were the same from day to day. Second, in our November field trip we marked all *A. fissifrons* on 5 *Cyrtophora* webs ($n = 31$) with enamel paint and monitored them once every 2 h between 2000 and 0600 h for 3 consecutive nights. Marked *A. fissifrons*'s body length, sex, and number of prey consumed, and the host webs' height of tangle, area of bowl, and number of prey caught were recorded. We performed Mann-Whitney U -tests to examine if mean body length and prey consumption rates (number of insects eaten per spider per hour) differed between individuals which stayed or left the host web during the observation. To assess whether *A. fissifrons* of different sexes differed in tenacity, we used a chi-squared test to examine the number of males and females between individuals which stayed and left the host webs.

Prey consumption by *Cyrtophora* and *A. fissifrons*

To assess if *A. fissifrons* spiders affected the food intake of the hosts, we compared the size distributions of prey consumed by them and their *Cyrtophora* hosts. Prey data were collected between March and May and between October and December 1997. During the field trips each night between 2000 and 0600 h, we monitored each marked *Cyrtophora* web once every 2 h, recording body length (mm) of prey successfully caught by the host and by *A. fissifrons*. *A. fissifrons*'s behavior in obtaining prey and the hosts' responses to the behavior of *A. fissifrons* were also recorded. In total, eighty-six prey

data were collected ($n = 45$ for *A. fissifrons* and 41 for *Cyrtophora* hosts) from 6 field trips. To assess whether or not *Cyrtophora* spiders and *A. fissifrons* consumed prey of similar size (as is in many *Argyrodex*-host systems), we performed a 2-sample Kolmogorov-Smirnov test to compare the size distribution of prey caught by both spiders. In addition, we also estimated the dry weight of the recorded prey using the length-weight regression equations provided by Schoener (1980) to determine the prey biomass intake from various size classes of prey. This may help determine if prey that can be potentially stolen by *A. fissifrons* represents a significant portion of total prey biomass intake of the hosts.

A. fissifrons was previously observed to approach both small prey trapped in the tangle threads and large prey being consumed by the host. In this portion of the study, we examined if *A. fissifrons* of different developmental stages foraged on different sizes of prey. As was mentioned previously, in the November field trip we marked all *A. fissifrons* in 5 *Cyrtophora* webs and measured their body lengths. During 3 nights of monitoring, we recorded the body lengths of those *A. fissifrons* approaching host prey. In the other field trips we did not mark *A. fissifrons*, but measured their body lengths when they were seen carrying small prey. Data from all field trips were combined, then a Mann-Whitney *U*-test was performed to examine if *A. fissifrons* approaching different sizes of prey differed significantly in body length.

RESULTS

The spiders

Two species of *Cyrtophora* (Araneidae) (Yaginuma 1986) can be found in the study site, building webs in shrubs or by tree trunks. Mature males (body length less than 4 mm) are much smaller than females and do not construct webs for foraging (I-Min Tso pers. observ.). These spiders are nocturnal, attacking prey items knocked down by the tangle threads and captured in the bowl web. The larger of the 2, *C. unicolor* (Doleschall 1857) (adult female body length about 20 mm), constructs a refuge composed of dried leaves several centimeters above the bowl web. The spiders hide in the refuge during the day, and emerge and hang inverted beneath the center of the bowl at night. The height of tangle scaffolds of webs constructed by mature females can reach 2 m, and the diameter of bowls may reach 1 m. Another host, *C. exanthematica* (Doleschall 1859)

(adult female body length about 15 mm), constructs webs similar to those of *C. unicolor* but of smaller size, and places its refuge beneath the bowl web. *C. exanthematica* also hides in the refuge during daytime and hangs inverted under the bowl web (not necessarily in the center) during night-time. Most of the observed activities of the hosts occur in the bowl webs, and only when severely disturbed will the spiders move up the tangle threads into the vegetation nearby.

Webs of both *C. unicolor* and *C. exanthematica* are frequently inhabited by numerous *Argyrodex fissifrons* (adult body length about 12 mm). The number of *A. fissifrons* on webs of *Cyrtophora* hosts ranged from 0 to more than 20. While at rest, *A. fissifrons* extends all its appendages and positions itself at various spots on the host webs. When those small prey items ignored by the hosts enter the web and cause vibration, the spider will move the 1st pair of walking legs in a rotary probing manner as it works its way toward the source of the vibration. After locating the prey, *A. fissifrons* will immobilize it by wrapping it with silk and then will carry the wrapped prey away from the host's web to feed. When the host subdues large prey and consumes it at the retreat, numerous *A. fissifrons* will move toward the prey in order to get a bite. If the actions of *A. fissifrons* disturb the host, the host usually deters them by shaking the web or pushing them away with its legs, then immediately resumes prey consumption. In addition to foraging, *A. fissifrons*' mating and ovipositing also occur in the host webs. We have seen mating take place in the tangle scaffold of host webs. In each of the 6 field trips, stringed egg-sacs produced by female *A. fissifrons* could always be found in some of the *Cyrtophora* webs. In addition to *Cyrtophora* hosts, *A. fissifrons* can also be seen in the tangle scaffold of webs spun by theridiid hosts in the study site. Another kleptoparasitic theridiid, *Argyrodex lanyuensis* (Yoshida et al. 1998), can sometimes be found in the webs of *Cyrtophora*, theridiids, and various species of orb-weaving spiders. However, *A. fissifrons* was never seen to invade webs spun by other orb-weaving hosts.

Population size of *A. fissifrons* and web space of *Cyrtophora* hosts

Data from 6 field trips were collected from 60 webs constructed by either *C. unicolor* or *C. exanthematica*. Because webs constructed by these 2 host species are similar in architecture but differ in size, we combined our data. There was a statistically significant positive relationship between body length of

Cyrtophora hosts and their (1) height of tangle ($r^2 = 0.515$, $F_{1,58} = 46.740$, $p = 0.000$, Fig. 1a) and (2) area of bowl web ($r^2 = 0.654$, $F_{1,58} = 83.231$, $p = 0.000$, Fig. 1b). A statistically significant positive relationship also existed between average number of *A. fissifrons* per web and (1) height of tangle ($r^2 = 0.335$, $F_{1,58} = 22.164$, $p = 0.000$, Fig. 2a) and (2) area of bowl web ($r^2 = 0.323$, $F_{1,58} = 20.947$, $p = 0.000$, Fig. 2b) of *Cyrtophora*, indicating that larger host webs were inhabited by more *A. fissifrons*.

Tenacity of *A. fissifrons* in webs of *Cyrtophora* hosts

Average numbers of unmarked *A. fissifrons* per host web per observation day in April, May, October, and December 1997 were not the same, but exhibited a certain amount of variation (Fig. 3). Among 5 *Cyrtophora* webs monitored in November, the percentage of marked *A. fissifrons* which stayed during 3 nights of observation ranged from 50% to 100%

($\bar{X} \pm SE = 73.6 \pm 18.0\%$). These results indicate that small amount of immigration/emigration by *A. fissifrons* occurs on a daily basis. Between *A. fissifrons* which stayed or left host webs, no significant difference was found in sex ratio (Pearson $\chi^2 = 0.036$, $df = 1$, $p = 0.849$), body length ($U = 117.000$, $p = 0.4316$), or prey consumption ($U = 117.000$, $p = 0.1783$).

Prey consumption by *Cyrtophora* and *A. fissifrons*

Results of a Kolmogorov-Smirnov 2-sample test showed that a significant difference existed between size distribution of prey consumed by *A. fissifrons* and by the *Cyrtophora* hosts (Kolmogorov-Smirnov 2-sample test statistic = 0.660, $p = 0.000$). The size of prey consumed by *A. fissifrons* ranged from 0.5 to 7.0 mm, and was significantly smaller than that by *Cyrtophora* hosts (3.3 ± 0.3 vs. 10.1 ± 1.2 mm). Although prey smaller than or equal to 7 mm constituted 46% of the hosts' total prey in number (Fig. 4a),

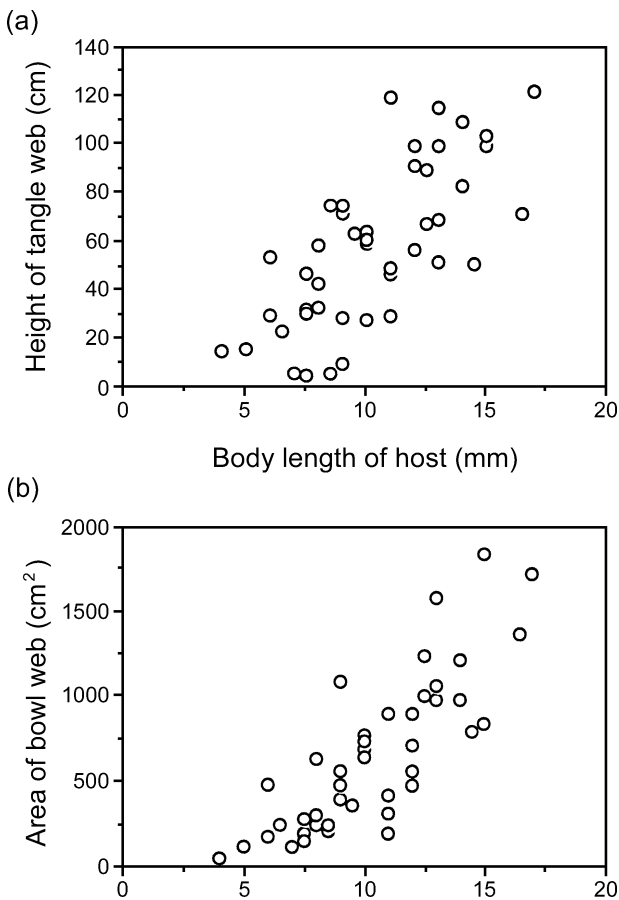


Fig. 1. The relationship between body length (mm) of *Cyrtophora* hosts and their height of tangle web (cm) (a) and area of bowl web (cm²) (b).

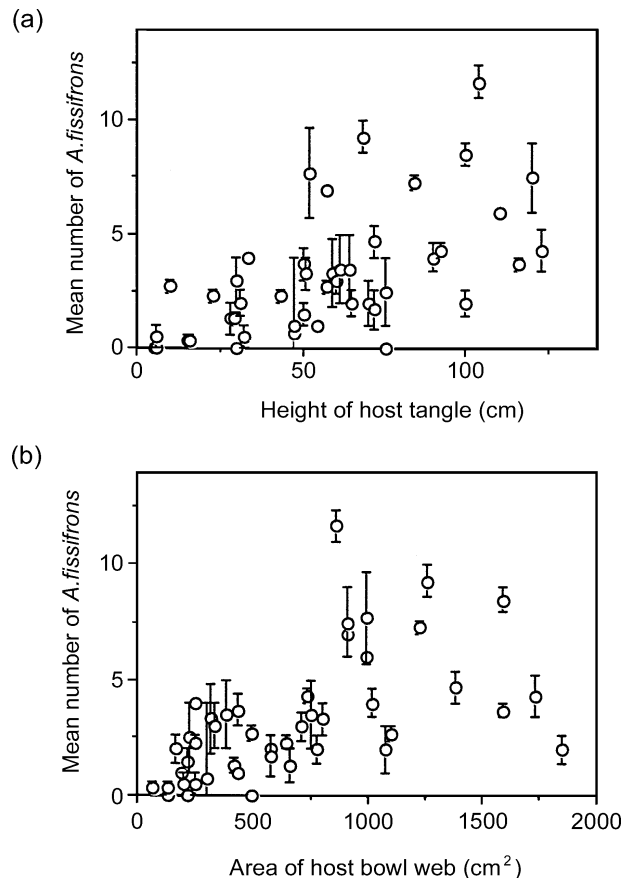


Fig. 2. The relationship between number ($\bar{X} \pm SE$) of inhabiting *Argyrodes fissifrons* and height of tangle web (cm) (a) and area of bowl web (cm²) (b) of webs spun by *Cyrtophora* hosts.

less than 10% of the hosts' prey biomass intake came from this size class (Fig. 4b). At the early stage of studies, we did not measure body length of *A. fissifrons* but only the size of prey they consumed. Therefore, among the 45 observed instances of prey consumption, only in 30 of them were body lengths of *A. fissifrons* recorded. From the November field trip, eighteen body length data were collected from those attempting to approach prey of the host. Results from a Mann-Whitney *U*-test indicated that those approaching host's prey were significantly larger than those approaching or carrying small prey (7.9 ± 0.5 vs. 6.1 ± 0.5 mm, $U = 368.5$, $p = 0.035$).

DISCUSSION

The relationship between population size of *Argyrodes fissifrons* and web size of *Cyrtophora* hosts resembles that between kleptoparasites and various spider hosts in many ways. Cangialosi (1990a 1990b) reported that the size of communal webs constructed by the social spider *Anelosimus eximius* correlated with the number of individuals inhabiting the web, and also correlated with the number of kleptoparasitic *Argyrodes ululans*. The work by Elgar (1994) on *Psecrus argentatus*, a tropical spider whose web is quite similar to that of *Cyrtophora*, showed that a positive correlation exists between inhabiting *Argyrodes fissifrons* and host webs' area of the lower sheet and height of the upper tangle. Elgar (1989) also reported that aggregating *Nephila edulis* webs were invaded by more *Argyrodes antipodanus* than were solitary ones; this phenomenon was described by him as a cost of aggre-

gation. Similarly, web space of *Cyrtophora* hosts correlated positively with number of inhabiting *A. fissifrons*. A larger web or web complex seems to be more easily located and colonized by wandering *Argyrodes* seeking appropriate habitat (Elgar 1989). In addition to size, age of hosts' webs seems to be another important factor determining number of inhabitants. Because building up a number of *A. fissifrons* on a given web takes time, newly-established webs may contain fewer inhabitants compared with older webs of the same size. This may explain why several large host webs contained relatively few *A. fissifrons* (Fig. 1b).

The population of *A. fissifrons* on webs of *Cyrtophora* can be characterized as a combination of fluid cluster and long-term association. Whitehouse and Jackson (1993) reported that *Argyrodes antipodiana* on webs spun by *Eriophora pustulosa* formed fluid populations, because individuals moved from web to web and did not seem to limit their activity to a

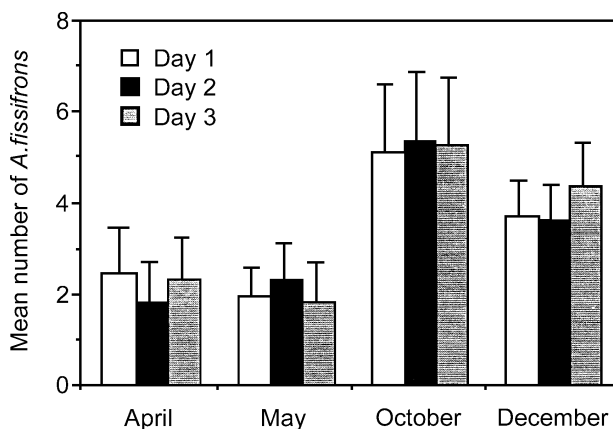


Fig. 3. Number ($\bar{X} \pm SE$) of *Argyrodes fissifrons* per *Cyrtophora* host web per day recorded from 4 field trips conducted in April, May, October, and December 1997.

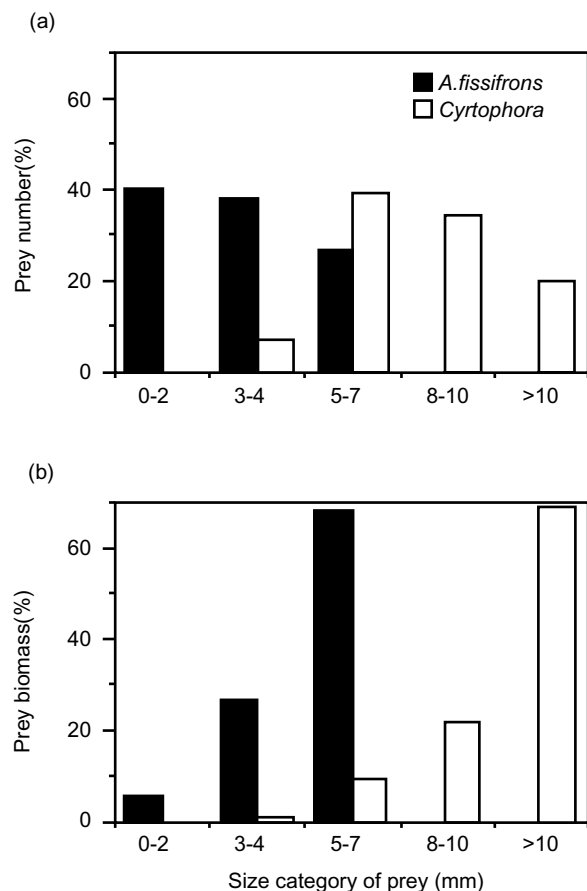


Fig. 4. Size distribution of prey consumed by *Cyrtophora* hosts ($n = 41$) and *Argyrodes fissifrons* ($n = 45$). (a) Percentage of prey number from each size class. (b) Percentage of estimated prey biomass from each size category.

particular host web. In this study, a small number of *A. fissifrons* was found to move in and out of host webs daily. This can be demonstrated by the fact that the average number of *A. fissifrons* per host web does not remain constant during each 3-d observation. However, a number of individuals seemed to stay in a given host's web, which can be shown by the consecutive presence of about 74% of marked individuals during our monitoring. Since *Cyrtophora* webs constitute the resting, foraging, mating, and reproduction sites of *A. fissifrons*, some individuals may have inhabited a particular web for a long period of time, mating and constructing their egg sacs there. However, a number of *A. fissifrons* still left the hosts' webs. From our November survey, the sex ratio, size, or prey consumption of individuals leaving the host webs did not differ from those that stayed. More effort is needed to elucidate the factors determining tenacity of *A. fissifrons* in host webs.

Results from this study indicate that food intake of *Cyrtophora* spiders does not seem to be severely affected by having *A. fissifrons* in their webs. *Cyrtophora* spiders, although not particularly large, can effectively subdue large prey due to their aggressiveness and complex web structure. The size of recorded prey consumed by *Cyrtophora* ranged from 3.5 mm to more than 30 mm, but that of *A. fissifrons* ranged only from 0.5 to 7 mm. When prey biomass was estimated, prey smaller than or equal to 7 mm constituted only < 10% of the total biomass intake of *Cyrtophora* spiders. Nevertheless, *Cyrtophora* is unlikely to lose that size category of prey to *A. fissifrons*. From more than 200 h of observations, we never observed *A. fissifrons* successfully acquiring prey being consumed by the hosts through stealing or robbing. However, we frequently observed *A. fissifrons* approach small prey trapped in the tangle or horizontal orb web then subdue it by wrapping it with silk. We have seen hosts being surrounded by up to 10 *A. fissifrons* while consuming prey. Hosts usually deter approaching *A. fissifrons* spiders by shaking the web or pushing them away with their legs from time to time. Therefore, it is quite possible that most prey items of *A. fissifrons* are those ignored or undetected by the host. *A. fissifrons* may cost the hosts by distracting them temporarily from feeding, but other than that they did not seem to significantly reduce the food intake of the host.

A. fissifrons may increase its diet breadth when it grows larger in size. On several occasions we have seen *A. fissifrons* carrying host prey remains. Since we never observed successful prey stealing or robbing, those prey appear to have been collected after the hosts had finished consumption. In this

study, the size of *A. fissifrons* observed approaching prey being consumed by the host is significantly larger than that observed carrying small prey items. This size-related foraging difference may have resulted from larger *A. fissifrons* going for both host prey remains and small prey, and smaller individuals concentrating more on small prey. Size and experience have been shown to greatly determine the outcome of social interactions in *Argyrodes* (Whitehouse 1997). Larger individuals tend to be more competitive in acquiring host prey remains than are smaller ones. Compared with fighting for large host prey remains, searching for small trapped prey is less competitive, therefore a better choice for smaller *A. fissifrons*.

This field study provides a basic understanding of the population variation, host web tenacity, and foraging of *A. fissifrons* inhabiting webs spun by *Cyrtophora* hosts. However, a removal experiment is absolutely necessary to unambiguously determine the mode of association between them. Only by a long-term field manipulation study, examining the effects of removal of either *A. fissifrons* or the hosts may we conclude with more confidence the nature of the interactions between them. However, given Orchid Island's severe weather conditions, which frequently destroy host webs, a considerable effort might be needed to gain sufficient long-term manipulation data.

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裂額寄居姬蜘蛛之族群特性及覓食行為研究

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本研究藉探討裂額寄居姬蜘蛛之族群特性及覓食行為來了解其對於雲斑蜘蛛宿主之影響。我們檢視：(一)裂額寄居姬蜘蛛之自然族群大小差異是否與宿主之網大小呈密切相關，(二)裂額寄居姬蜘蛛是否長期依附於某些宿主之網上，以及(三)裂額寄居姬蜘蛛之覓食行為是否會影響宿主之攝食。於蘭嶼所進行之野外調查結果顯示，宿主網之障礙網(tangle barrier)高度及水平皿網(bowl web)之面積與寄居其中之裂額寄居姬蜘蛛平均數呈顯著之正相關。每一宿主網上之裂額寄居姬蜘蛛平均數每日不同，顯示有若干數目之該種蜘蛛每日於宿主網上進出。但是，根據連續三夜對被標定個體所進行之觀察，平均有70%以上之個體停留於特定之宿主網內。停留於宿主網內之裂額寄居姬蜘蛛與離開者在性別比例、攝食量及體型上並無顯著差異。宿主與裂額寄居姬蜘蛛在所攝入之獵物體長分布上有極顯著之差異，且前者所攝取之獵物平均體長遠大於後者。這些結果顯示裂額寄居姬蜘蛛之主要食物來源為宿主不會攝食之小型獵物，因此該蜘蛛應不會對宿主之攝食造成顯著影響。

關鍵詞：裂額寄居姬蜘蛛，雲斑蜘蛛，蘭嶼，蜘蛛。

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