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Author(s): Mark A. Elgar

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Experimental evidence of a mutualistic association between two web-building spiders

MARK A. ELGAR

Department of Zoology, University of Melbourne, Parkville, Victoria 3052, Australia

Summary

1. The large sheet- and tangle-webs of the tropical spider *Psecchrus argentatus* provide structural support to two small spiders, the orb-weaver *Philoponella undulata* and the kleptoparasite *Argyrodes fissifrons*. In general, larger host webs have more guests than smaller host webs.

2. The growth rate of *P. argentatus* was reduced, apparently as a result of lower food intake rates, when individuals of *P. undulata* were experimentally excluded from the host web. The control spiders may have had higher food intake rates because the webs of *P. undulata* attract more prey items and/or increase the probability that prey fall into the sheet-web of *P. argentatus*. These field experiments, together with field observations, indicate that the relationship between *P. argentatus* and its web guest *P. undulata* is mutualistic. Mutualistic relationships between two species of spiders have not been previously recorded.

3. The higher growth rate of *P. argentatus* with *P. undulata* guests may substantially enhance the reproductive success of the host spider, either through reducing the time taken to form a clutch of eggs, or increasing the clutch size.

4. When *P. argentatus* was experimentally removed from its web, the numbers of *P. undulata* and *A. fissifrons* dropped, and eventually no guests were found in the web complex. Experimental manipulation of the number of each guest species per web and observations of natural populations, revealed no correlation between the numbers of each guest species per host web.

Key-words: *Argyrodes*, field experiments, kleptoparasitism, mutualism, *Philoponella*, *Psecchrus*, spiders.

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Introduction

The webs of many species of spider are host to a diversity of other spiders and insects, including flies, damselflies, wasps and moths that co-exist apparently unharmed (see Vollrath 1984, 1987; Nentwig & Heimer 1987; Common 1990). Most early accounts of these associations are anecdotal and the relationships usually described as commensal: the guest benefits from the relationship, but the host neither benefits nor suffers a cost. More recent studies indicate that some of these associations are more appropriately termed kleptobiotic (e.g. Vollrath 1987), because the guests obtain their food from prey caught in the web of the host spider. These spider kleptoparasites are represented in at least four families (Dictynidae, Mysmenidae, Symphytognathidae and Theridiidae), and those belonging to the genus *Argyrodes* (Theridiidae) are among the more extensively documented (see

Vollrath 1984, 1987; Elgar 1993). Although indirect evidence suggests a kleptoparasitic relationship, there are no experimental data demonstrating that the growth rate or fecundity of the host is reduced by the presence of the kleptoparasites (see Elgar 1993).

Mutualistic associations that include spiders are rare compared with the widespread occurrence of these associations in other taxa (e.g. Boucher, James & Keeler 1982; Boucher 1985; Janzen 1985; Smith & Douglas 1987; Hölldobler & Wilson 1990; Huxley & Cutler 1991). Tietjen, Ayyagari & Uetz (1987) report that social spiders *Mallos gregalis* (Dictynidae) do not remove the remains of prey from their nest; instead, these prey debris become a nutritional base for various yeasts. The odour of the yeast is apparently attractive to various flies that settle on the yeast and are subsequently caught by the spiders. The relationship between spider and yeast appears to be mutualistic because the spiders provide food for the yeast, and

the yeast attracts the spiders' prey. Shepard & Gibson (1972) describe an apparently mutualistic relationship between the salticid spider *Cotinus* and the dolichoderine ant *Tapinoma melanocephalum*. In this association, the spider uses the ant nest as a foundation for building its web and, in return, provides the ants with some protection from predators and parasites. Many other species of spiders live in or near ants' nests, and perhaps some of these associations are also mutualistic (see Elgar 1993). Interestingly, there are no records of mutualisms between two species of spider, perhaps reinforcing the view that spiders form competitive or predatory relationships.

In the rainforests and secondary successional forests of Madang Province, Papua New Guinea, the webs of the sheet-web spider *Psecchus argentatus* Doleschall (Psecchidae) are frequently host to two other species of spiders, an uloborid *Philoponella undulata* Thorell and a theridiid *Argyrodes fissifrons* O. Pickard-Cambridge. *Psecchus argentatus* is a large (<8 cm) spider that builds a substantial web complex comprising a sheet-web which is supported above by a tangle of threads that form a barrier-web. Prey items are captured by this fast-moving spider when they either fall directly into the sheet-web or are deflected onto the sheet-web from the barrier-web. Further details of prey-capture behaviour and other details of the biology of *P. argentatus* are provided by Robinson & Lubin (1979).

The uloborid and theridiid guests are usually found in the barrier-web of *P. argentatus*; *P. undulata* is a small (<0.8 cm) orb-web spinning spider that uses the tangle threads of the host web as support structures for its orb-web. The slightly larger (<1.5 cm) species, *A. fissifrons*, does not build a web, but instead patrols the barrier threads and very occasionally ventures onto the sheet-web. There is little, if any, behavioural interaction between the host spider and the guests. The host remains in a retreat or under the sheet-web where it captures prey (see Robinson & Lubin 1979), and only ventures onto the barrier-web to repair the barrier-web. Neither guest spider appears to be host specific: *A. fissifrons* is found on the webs of several species (see, for example, Tanaka 1984), and *P. undulata* is found on the webs of *Cyrtophora* sp. and other agelenid spiders (Lubin 1986).

The aim of this study was to establish experimentally the nature of the relationship between the host spider *P. argentatus* and its two guests *P. undulata* and *A. fissifrons*. The latter is usually described as a kleptoparasite, obtaining food by stealing prey from the web of other spiders, and some individuals may even capture the host spider (see Tanaka 1984). Many species of *Philoponella* are described as commensals, benefiting from living in the web of their host through using the barrier-web threads as supports for their orb-webs, but not imposing any cost on the host spider (e.g. Lubin 1986). However, no previous study has

attempted to examine experimentally the costs and benefits of the relationship to the participants.

Methods

The study population of *P. argentatus* and its guests was located in an 'old garden' on the slopes of Nobanob Hill (elevation 300 m), near the Christensen Research Institute, Madang Province, Papua New Guinea. The re-growth forest in this garden was dominated by *Macaranga* sp. (Euphorbiaceae), *Piper* sp. (Piperaceae) and *Ficus* sp. (Moraceae) (M. Jebb pers. comm.). Observations and experiments were conducted from July to September, 1989 and February to March, 1993. The garden supported a large population of *P. argentatus* in 1989, although the species appeared to be less abundant in 1993.

Web characteristics and the numbers of each species of guest per web were obtained by censusing a sample of the population on a single day. Webs of *P. argentatus* were selected haphazardly, while attempting to maximize variation in web size. The following data were obtained: the length and width of the sheet-web; the height of the tangle-web (the distance from the sheet-web to the top of the tangle-web); and the number of *P. undulata* and *A. fissifrons* on or attached to the host web. The host spiders were removed from their webs and transported to the Christensen Research Institute, where they were weighed to the nearest 0.01 g. The spiders were subsequently released back onto their webs at the study site. Several females of *P. argentatus* with egg sacs were discovered during the course of the study, and these females, together with their egg sacs, were weighed and the numbers of eggs counted.

The effects of the presence of each species of spider on the other two species were examined in four experimental manipulations. In each experiment a number of webs of *P. argentatus* was located and assigned randomly as either control or experimental. The first experiment investigated whether the presence of the host influenced the number of guests on the web. For the experimental treatment, each *P. argentatus* was removed from its web and released elsewhere. Each control *P. argentatus* was removed and then carefully released back onto its web. Considerable care in removing and replacing each spider was essential to minimize damage to the web, and ensure that the spider remained on its web after manipulation. About 80% of the control spiders were present on their webs the following day. The numbers of both *P. undulata* and *A. fissifrons* on five control and five experimental host webs were recorded every day, for the next 4 days. The structural integrity of the experimental webs had obviously deteriorated by that time.

The second experiment investigated whether an increase in the number of *A. fissifrons* per host web influenced the number of *P. undulata* or induced *P. argentatus* to abandon its web. Five *A. fissifrons* were

added to each of ten experimental webs of *P. argentatus* and a further 10 webs were used as controls. The presence or absence of *P. argentatus*, and the numbers of *A. fissifrons* and *P. undulata* on each web, were recorded over the next 4 days.

A third set of experiments examined the effects of the presence of *P. undulata* and *A. fissifrons* on the growth rate of the host, *P. argentatus*. These experiments followed the same general procedure: webs of *P. argentatus* were located haphazardly and then categorized as either control or experimental spiders. Each *P. argentatus* was removed from its web, weighed to the nearest 0.01 g, and carefully placed back onto its sheet-web (see above). In all trials, the relevant guests were removed from both control and experimental webs, but guests on control webs were immediately replaced. The webs of both experimental and control spiders were then censused each day until the end of the experimental period, and the following data were collected: numbers of each guest species per web, and whether the host spider had captured, or was feeding on, a prey item. Invariably, these prey items were too badly deteriorated to allow accurate identification. Any guest spiders found on experimental webs during the experimental period were removed. The host spiders were weighed at the end of the experimental period. Ten control and ten experimental host webs were selected for the first trial, in which both *A. fissifrons* and *P. undulata* were removed from the host webs, and the experiment lasted 7 days. The same procedure was followed in the second trial, except that 20 control and 20 experimental host webs were selected, and the experiment lasted 16 days. In the final trial, 20 control and 20 experimental host webs were selected, but only *P. undulata* were removed, and the experiment lasted 14 days.

The measures of host weight were log transformed in order to normalize distributions, and all data were analysed using SYSTAT 5.2 for the Apple Macintosh (Wilkinson 1992). Where appropriate, Bonferroni corrections were applied to probability values.

Results

NATURAL VARIATION IN THE NUMBER OF GUESTS

The numbers of *P. undulata* and *A. fissifrons* found on the sample of 24 host webs of *P. argentatus* varied; some host webs were free of any guests, but as many as 19 *P. undulata* and 10 *A. fissifrons* were observed on single webs. The mean number of *P. undulata* per web was 8.2 (SE = 0.9) and of *A. fissifrons* per web was 4.3 (SE = 0.7). Larger *P. argentatus* built larger webs; there were significant positive correlations between the weight of *P. argentatus* and both the area of the sheet-web ($r = 0.83$, $P < 0.001$, $n = 24$) and the height of the upper tangle-web ($r = 0.65$, $P < 0.01$, $n = 24$). In general, larger webs were hosts to greater numbers of *P. undulata* and *A. fissifrons*. The number

of *P. undulata* per web was significantly correlated with the height of the tangle-web (Fig. 1a), but not with either the weight of the host ($r = 0.48$, ns, $n = 24$) or the area of the sheet-web ($r = 0.55$, ns, $n = 24$). In contrast, the number of *A. fissifrons* per web was significantly correlated with the area of the sheet-web (Fig. 1b) and the weight of the host ($r = 0.72$, $P = 0.001$, $n = 24$), but not the height of the tangle-web ($r = 0.44$, NS, $n = 24$). There was no correlation between the numbers of *A. fissifrons* per web and *P. undulata* per web ($r = 0.31$, NS, $n = 24$).

REMOVING THE HOST

Individuals of *P. undulata* at Nobanob Hill were never found on the webs of other spiders, nor among the vegetation. Elsewhere in the Madang region, the orb-weaver *Cyrtophora* sp. was sometimes host to *P. undulata*: the former builds a large, relatively permanent horizontal orb-web with a tangle-web above (see also Lubin 1986). Similarly, *A. fissifrons* was never encountered in the vegetation; it was usually found on the web of *P. argentatus*, but has also been recorded on the webs of other spiders (e.g. Tanaka 1984).

Experimental removal of *P. argentatus* from their webs resulted in a rapid reduction in the numbers of *P. undulata* and *A. fissifrons* per host web (Table 1).

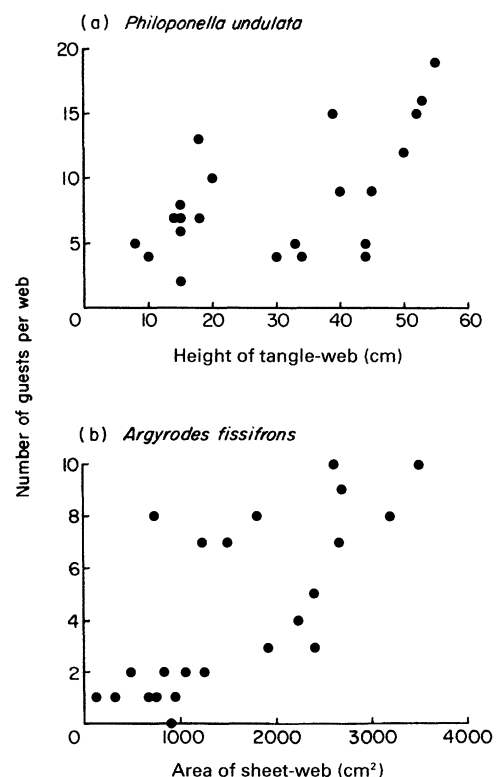


Fig. 1. The number of each species of guest per host web varies according to different host web characteristics: (a) the abundance of *P. undulata* per host web is positively correlated with the height of the tangle-web ($r = 0.59$, $P < 0.05$, $n = 24$), while (b) the abundance of *A. fissifrons* per host web is positively correlated with the area of the sheet-web ($r = 0.74$, $P = 0.001$, $n = 24$).

Table 1. Changes in the number of spider guests, *Philoponella undulata* and *Argyrodes fissifrons* per web following removal of the host *Psechrus argentatus*

		Following manipulation†			
		Day 1	Day 2	Day 3	Day 4
<i>P. undulata</i>					
control	6.0	7.6	8.0	6.0	7.6
	(0.3)	(1.4)	(1.6)	(1.8)	(1.9)
host removed	8.4	3.6	3.4	2.2	2.4
	(1.2)	(0.5)	(0.9)	(0.5)	(1.2)
<i>A. fissifrons</i>					
control	4.8	4.0	4.2	3.4	2.8
	(1.2)	(0.9)	(0.9)	(0.8)	(1.2)
host removed	5.0	3.0	1.4	0.6	0.4
	(1.1)	(0.9)	(0.7)	(0.4)	(0.4)

†Values are mean number of guests, with standard errors in parentheses, derived from five control and five experimental webs.

Repeated-measures ANOVA of the number of *P. undulata* on the web on the successive days after the host had been removed revealed a significant treatment (between-subjects) effect ($F_{1,8} = 10.68$, $P = 0.01$), but no significant time (within-subjects) effect ($F_{3,24} = 0.93$, NS) or interaction ($F_{3,24} = 0.17$, NS). A similar analysis of the numbers of *A. fissifrons* per web yielded a significant between-subject treatment effect ($F_{1,8} = 5.74$, $P < 0.05$) and within-subjects time effect ($F_{3,24} = 7.16$, $P = 0.01$), but no significant interaction ($F_{3,24} = 1.16$, NS). Thus, while the number of both guests decreased following host removal, the number of *P. undulata* per web, unlike that of *A. fissifrons*, did not subsequently decrease further. However, it is difficult to interpret this difference between the species because the number of *A. fissifrons* became lower in both control and experimental treatments.

REMOVING THE GUESTS

In all three experiments, the growth rate of *P. argentatus* tended to be consistently higher if *P. undulata* were present in the barrier-web than if these guests were absent (Fig. 2). Analysis of covariance (with

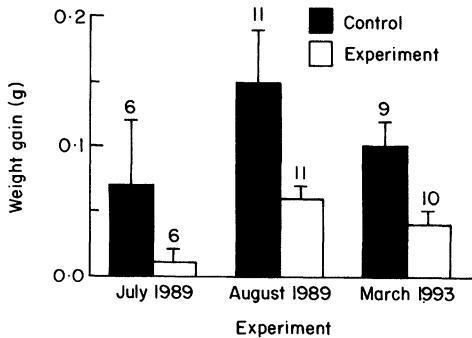


Fig. 2. The host spider *P. argentatus* has a significantly greater rate of weight gain when guests are present (control) compared with when they are removed (experimental). Both *A. fissifrons* and *P. undulata* were removed in the 1989 experiments, but only *P. undulata* was removed in the 1993 experiment. Values are means with sample sizes given above the standard error bars. See text for statistical tests.

treatment as the factor and initial host weight as the covariate) of data from the first experiment, that lasted for only 7 days, revealed no significant difference in the weight of *P. argentatus* with or without their guests (treatment: $F_{1,9} = 1.20$, $P > 0.3$; initial weight: $F_{1,9} = 0.33$, $P > 0.5$). The same analysis of data from the subsequent experiment, which had more replicates and lasted longer, revealed a trend: *P. argentatus* with guests had higher growth rates than those without (treatment: $F_{1,18} = 3.59$, $P = 0.07$; initial weight: $F_{1,18} = 0.52$, $P > 0.4$). However, it was not possible to determine from this experiment whether *P. undulata* or *A. fissifrons* was responsible for the difference in growth rates. The final experiment revealed that the difference was due to the presence of *P. undulata*: control *P. argentatus* whose webs were host to this guest gained significantly more weight than did their experimental counterparts (treatment: $F_{1,16} = 5.73$, $P = 0.03$; initial weight: $F_{1,16} = 14.78$, $P = 0.01$). The weight gain of control *P. argentatus* was significantly correlated with the average number of *P. undulata* per host web (Fig. 3), but not with the number of *A. fissifrons* per host web ($r = 0.355$, $n = 20$), a pattern that was consistent with the experimental results.

The difference in weight gain in *P. argentatus*

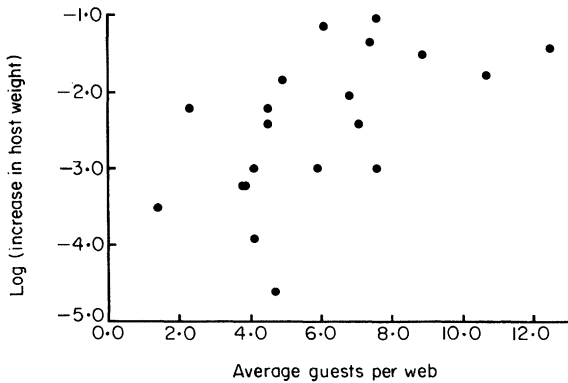


Fig. 3. The rate of weight gain by *P. argentatus* is significantly correlated with the average number of *P. undulata* guests per web ($r = 0.575$, $P < 0.01$, $n = 20$).

between treatments is most likely to be due to differences in prey-capture rates. Combining the census data across the three experiments, but ensuring that the frequency with which control and experimental webs were censused was the same (between 3 and 5 days), revealed that 61% ($n = 26$) of hosts with guests captured at least one prey item, compared with 27% ($n = 26$) of hosts without guests ($\chi^2 = 4.99$, $df = 1$, $P = 0.03$).

The greater weight gain experienced by *P. argentatus* with guests may result in substantial fitness benefits. On average, an egg mass of *P. argentatus* weighs 0.3 g ($SD = 0.1$, $n = 5$) and contains 184 eggs ($SD = 71$, $n = 5$), representing about 38% of the female's body weight. Thus, the difference in weight gain (about 0.05–0.09 g) between control and experimental *P. argentatus* over a period of 10–14 days, is roughly equivalent to 10–20 eggs. This difference in reproductive output may be substantially greater over the longer period of time required to form a complete clutch of eggs.

INTERACTIONS BETWEEN GUESTS

On two occasions, an individual of *A. fissifrons* was observed feeding on an individual of *P. undulata*, suggesting that *A. fissifrons* is a predator of *P. undulata*. Although individuals of *A. fissifrons* will move toward those of *P. undulata*, sometimes venturing onto their webs, successful predatory attacks were not observed in over 10 h observation of four different host webs. Nevertheless, both species react aggressively when confronted with either conspecifics or members of the other species. An individual of *P. undulata* shakes its web if approached by *A. fissifrons*, and *A. fissifrons* shakes the structural threads when it encounters another *A. fissifrons*.

Experimental manipulation of the numbers of each guest species per host web had no influence on the number of the other guest species per host web (Table 2). An analysis of covariance of the average change in the number of guests per web over a 4-day period, with treatment as the main factor and initial number of guests as the covariate, revealed that adding individuals of *A. fissifrons* to the webs of *P. argentatus* had no effect on the subsequent numbers of *P. undulata* (treatment: $F_{1,14} = 1.14$, NS; initial number: $F_{1,14} = 6.70$, $P < 0.05$). Similarly, experimental removal of *P. undulata* from host webs had no effect on the subsequent numbers of *A. fissifrons* (treatment: $F_{1,14} = 0.55$, NS; initial number: $F_{1,14} = 35.69$, $P < 0.05$). These results are not surprising, given the absence of a significant correlation between the numbers of *A. fissifrons* and *P. undulata* on natural host webs (see above).

Discussion

The experiments described here reveal that the sheet-web spider *Psechurus argentatus* benefits from the pres-

ence of *Philoponella undulata* as guests in its web complex, suggesting that the relationship between these two species is mutualistic. Individuals of *P. argentatus* with *P. undulata* as guests have higher growth rates than do those whose guests have been removed, apparently as a result of increased rates of food intake. Such a mutualistic relationship between two species of spider has not been previously demonstrated. The difference in rates of weight gain between control and experimental spiders represents a substantial number of eggs, suggesting that the presence of these spider guests may influence the reproductive output of the host spider. *Psechurus argentatus* with guests may either increase reproductive output within a given time period, or reduce the amount of time required to form a clutch of eggs. It is not known whether females of *P. argentatus* produce several clutches of eggs during their lifetime.

There are at least two mechanisms by which the presence of *P. undulata* might increase the rates of food intake of *P. argentatus*. First, the guests may increase the encounter rate between prey and the host web, and hence the probability of capturing an insect. The webs of many spiders, including *Philoponella*, contain silk that has high UV-reflectance properties, which may increase insect–web encounter rates (Craig & Bernard 1990; Craig 1991) as a result of the insects' tendency to fly toward UV-light (e.g. Silberglied 1979). *Psechurus argentatus* with guests may therefore obtain more prey because the webs of their guests attract more insects. Second, the additional silk and webs produced by *P. undulata* may increase the chances of a prey item falling into the sheet-web of the host, in a way analogous to the ricochet effect described for social spiders (Rypstra 1985; Uetz 1986, 1989). Insects attempting to avoid an orb-web built by *P. undulata* may be more likely to encounter yet another orb-web and eventually the host's sheet-web. Of course, it is possible that *P. argentatus* may lose some prey items that are caught in the orb-webs of *P. undulata*. However, these prey items are likely to be small, and, in any case, the amount of prey lost in this way must be lower than that gained by the presence of the guests because there was a net weight gain by the hosts in the presence of *P. undulata*.

It is also possible that *P. argentatus* with *P. undulata* gain more weight because individuals of *P. argentatus* actively seek out and capture these guests. Although this interpretation cannot be rejected, it seems unlikely for several reasons. First, *P. undulata* are very small, and hence large numbers would have to be consumed to yield the difference in weights. Second, *P. argentatus* capture prey that are arrested by the sheet-web (see also Robinson & Lubin 1979), and rarely move along the tangle threads of the barrier-web. Similarly, individuals of *P. undulata* were never seen in or near the sheet-web.

The benefits of this relationship to the orb-weaver *P. undulata* could not be quantified because this spider

Table 2. The effects of (a) adding *A. fissifrons* to the host web on the number of *P. undulata* per web and (b) removing *P. undulata* from the host web on the number of *A. fissifrons* per web. Values are means, with standard errors in parentheses. See text for statistical analyses

	Number of guests per host web	
	Control	Experimental
(a) Add five <i>A. fissifrons</i> per web		
number of host webs	9	8
initial <i>P. undulata</i>	7.4 (0.9)	9.3 (0.7)
average <i>P. undulata</i> over 4 days	8.2 (0.6)	8.0 (0.9)
(b) Remove <i>P. undulata</i>		
number of host webs	11	11
initial <i>A. fissifrons</i>	1.6 (0.6)	2.2 (0.6)
average <i>A. fissifrons</i> over 4 days	1.5 (0.4)	1.6 (0.3)

appeared to be obligately associated with *P. argentatus* at Nobanob Hill. Although the webs of *P. undulata* were observed elsewhere within the barrier-webs of other host spider species, including *Cyrtophora*, *P. undulata* apparently never spins its web independently of a host spider. Furthermore, *P. undulata* will eventually leave the host web if it is damaged, or covered in leaves and other debris, or if the host is no longer present. *Philoponella undulata* is a colonial species, and individuals sometimes share structural threads; perhaps the barrier-web provides sufficient attachment sites that allow the spiders to build webs in close proximity. The positive correlation between the number of guests per web and the height of barrier-web suggests that the size of the barrier-web places an upper limit on the number of *P. undulata*. Additionally, these attachment sites may remain secure, at least while the host maintains the structure of its web. The latter benefit may explain why *P. undulata* leave the web if the host disappears.

The relationships between *A. fissifrons* and both *P. argentatus* and *P. undulata* are not clear; individuals of *A. fissifrons* patrolled the barrier-web and were rarely seen near or on the sheet-web. Larger numbers of *A. fissifrons* were found on the webs of larger host spiders with larger sheet-webs, but not necessarily larger barrier-webs. Thus, the numbers of *A. fissifrons* may be limited by food availability, rather than space, because larger sheet-webs may arrest more prey, some of which may be stolen by *A. fissifrons*. *Argyrodes fissifrons* could have a negative impact on *P. argentatus* in several ways; first, its kleptoparasitic lifestyle may reduce the food intake rate of *P. argentatus*. Second, individuals of *A. fissifrons* were observed feeding on the corpses of *P. undulata* on at least three occasions, and once on *P. argentatus* (L. Higgins, pers. comm.), although it is not known whether *A. fissifrons* captured these spiders. If *A. fissifrons* preys

on *P. undulata*, then it has an indirect negative effect on *P. argentatus*. The lack of correlation between the numbers of *P. undulata* and *A. fissifrons* per web suggests that the kleptoparasites do not depend primarily on *P. undulata* as a source of food (cf. Elgar 1989).

The study raises the more general question of how these spider guests or associates locate the webs of their hosts. This is particularly relevant for those guests that are obligately associated with their hosts, such as *P. undulata*. For example, the webs of *P. argentatus* are often damaged as a result of heavy rain or foliage falling on the web. Although *P. argentatus* may repair some of its web, badly damaged webs are abandoned by the host. The guests eventually follow suit and must then locate a new host web. The presence of *P. undulata* on the webs of *P. argentatus* and other hosts that are widely dispersed or at low density suggests that *P. undulata* may be using specific cues to find these webs rather than encountering them haphazardly. An obvious cue would be chemicals that are released from the silk. The host spiders may even vary the concentrations of these pheromones, according to the number of individuals of *P. undulata* in the tangle web.

Spiders are frequently described as food-limited, generalist predators, with widely overlapping diets that often include individuals of other spider species. This observation has prompted many ecologists to assume that competition and predation are the principal kinds of interactions in spider communities (but see Wise 1993). One consequence of this perception is that mutualisms involving spiders have been rarely investigated. While the Araneae may be characterized by an absence of mutualisms, other mutualistic associations may await detection; for example, several species of *Philoponella* are commonly found on the webs of other spiders (Lubin 1986), and the relationship between these spiders and their hosts may also be

mutualistic. There is also the possibility that non-mutualistic associations have been incorrectly inferred. As with other organisms, field experimentation will be the most direct method of uncovering these and other unexpected ecological relationships.

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