

**POPULATION CHARACTERISTICS OF A KLEPTOPARASITIC SPIDER
ARGYRODES FLAVESCENS (ARAENAE: THERIDIIDAE) AND
ITS IMPACT ON A HOST SPIDER *NEPHILA PILIPES*
(ARANEAE: TETRAGNATHIDAE) FROM SINGAPORE**

Teck Hui Koh and Daiqin Li

*Department of Biological Sciences, National University of Singapore, 10 Kent Ridge Crescent,
Singapore 119260. Email: dbslidq@nus.edu.sg*

ABSTRACT. – *Argyroides flavescens* is a common theridiid spider species foraging in the web of a host spider *Nephila pilipes* in Singapore. In the present study, we investigated the factors that influence the relationship between kleptoparasites and host spiders and the impact of kleptoparasites on hosts. Field surveys were conducted to examine how host size, web size, and ambient light intensity around webs affect the abundance of *A. flavescens*. The results from the field study showed that the mean number of *A. flavescens* is positively correlated with body size and web size of host spiders, and ambient light intensity surrounding the webs. Laboratory experiments were carried out to examine the impact of *A. flavescens* on *N. pilipes* by manipulating the number of *A. flavescens* present on the webs. The experimental results demonstrated that *A. flavescens* reduces host weight gain, increases mortality of host spiders, rate of web relocation, and web damage. These findings suggest that *A. flavescens* is detrimental to host spiders, *N. pilipes*, by stealing freshly captured prey items from the host, forcing the hosts to relocate the webs more frequently, sharing the large prey item with the host, and removing large quantity of silk from the host web.

KEY WORDS. – *Nephila pilipes*, *Argyroides flavescens*, spider, kleptoparasite, silk stealing, Singapore.

INTRODUCTION

A spider web represents a unique microhabitat which provides a variety of resources, such as captured prey, prey remains, silk, eggs, juveniles and adults of spiders, thus attracting many parasitoids, predators, or kleptoparasites. The theridiid spiders of the genus *Argyroides* are well known to live in close association with large web-weaving spiders, and they exploit the resources on the webs by a wide range of foraging strategies. They may be either commensal (collecting small prey apparently ignored or prey remains abandoned by hosts) (e.g., Exline & Levi, 1962; Tso & Severinghaus, 2000), kleptoparasitic (stealing prey freshly captured and stored by hosts) (e.g., Vollrath 1979; Rypstra, 1981; Cangialosi, 1991), araneophagic (eating host spider adults or juveniles) (e.g., Kullmann, 1959; Smith Trail, 1981; Wise, 1982; Tanaka, 1984; Larcher & Wise, 1985; Whitehouse, 1986; Grostal & Walter, 1997), or

oophagous (feeding on eggs) (Pasquet et al., 1997). Many species, however, actually switch between foraging strategies (for review, see Elgar, 1993). For a given species of *Argyroides*, what foraging strategy an individual will adopt generally depends on the resource availability on the web. Although the studies regarding the interactions between *Argyroides* and spider hosts are abundant, how population of *Argyroides* changes and how population changes affect kleptoparasite-host interactions are poorly understood.

The *Argyroides*-host relationships may vary from time to time with host spider species, life stage and sex of host species, web characteristics, prey availability, and environmental conditions. It is well known that the abundance of *Argyroides* considerably varies among and within host species (for review, see Elgar, 1993). In addition, the abundance of *Argyroides* is also influenced by web characteristics, such as the

size, structure and occupancy of host webs (e.g., Whitehouse, 1988; Grostal & Walter, 1999; Henaut, 2000; Tso & Severinghaus, 2000). In general, large, vertical orb webs with barrier webs tend to be parasitized by more *Argyrodes*. Many environmental conditions can also affect the prey type and abundance, and in turn, determine the host web distribution and density. A majority of studies have been conducted on *Argyrodes* species from America, neotropics, and Australia (see Elgar, 1993), but there have been fewer detailed studies of relationships between *Argyrodes* species of East Asia and their host spiders (*Argyrodes fissifrons/Agelena limbata* from Japan: Tanaka, 1984; *A. lanyuensis/Nephila pilipes* (formerly *N. maculata*) from Taiwan: Tso & Severinghaus, 1998; *A. fissifrons/Cyrtophora* from Taiwan: Tso & Severinghaus, 2000; *A. bonadea* and *A. flavescens/Nephila clavata* from Japan: Miyashita, 2001). However, nothing is known of these *Argyrodes*-host interactions in South-east Asia.

Argyrodes flavescens (O. P.-Cambridge) commonly distributes in tropical and subtropical Asia, and has long been known as a kleptoparasitic spider inhabiting on webs of the giant wood spider *Nephila pilipes* (Fabricius) in Singapore (Koh, 1989). However, there is no published work examining the association of these two particular species. In addition, the actual relationship between *A. flavescens* and *N. pilipes* as well as the potential impact of *A. flavescens* on *N. pilipes* is not clear. Furthermore, the *A. flavescens*-*N. pilipes* is an ideal system for investigation of the interactions and potential impact of these interactions because both species are very abundant in Singapore, enabling the field observations and experimental manipulations to be made relatively easily. The present study is the first step toward the understanding of behavioural interactions between these two particular species. We conducted field surveys to examine whether the abundance of *Argyrodes flavescens* was correlated with host spider size, web size of *Nephila pilipes*, and environmental factors such light intensity. We also conducted laboratory experiments to investigate how *A. flavescens* affected mortality, weight gain, web damage and web relocation of *N. pilipes*. We predicted that 1) the abundance of *A. flavescens* was positively correlated with host body size, web size and light intensity; 2) *A. flavescens* increased juvenile mortality of *N. pilipes*, 3) *A. flavescens* reduced weight gain in *N. pilipes*, and 4) *A. flavescens* increased web damage and web relocation of *N. pilipes*.

METHODS

Field study

The field study aimed to determine how abundance of *Argyrodes flavescens* would be affected by body size of *Nephila pilipes*, web size, and light intensity surrounding the webs. We conducted the field surveys between 0800 and 1600 h from December 1998 to June 1999 in the Bukit Timah Nature Reserve, Labrador Park, and Yishun in Singapore. The Bukit Timah Nature Reserve (75 ha) retains the only patch of dipterocarp-dominated primary (undisturbed) forest and is linked by secondary forests to the Central Catchment Area. Labrador Park is a hill sea-facing 12-hectare park with a secondary forest. The site at Yishun is a forest consisted of a variety of fruit trees and has been abandoned for about 10 years.

During the study, we searched each site for webs of *Nephila pilipes* (juveniles and adult females) and associated *Argyrodes flavescens* up to a height of 2.5 m above ground level. For each *N. pilipes* sighted, we collected the following data: body length (cm) (measured from the chelicerae to the end of abdomen, excluding spinnerets), web size of *N. pilipes*, numbers of *A. flavescens* in the webs of *N. pilipes* if any, and light intensity (lux) surrounded the *N. pilipes* webs. To measure the body length of *N. pilipes*, we removed the spiders from the webs and released them back into the webs after measuring. To determine the web size, we measured the maximum horizontal and vertical diameters (cm) of each web from the outer-most sticky spirals. The web area was then calculated as: web area = $\pi \times 1/2$ vertical diameter $\times 1/2$ horizontal diameter.

Laboratory experiments

We conducted laboratory experiments to examine the effect of *Argyrodes flavescens* on mortality, weight gain, web damage and web relocation of the host spider *Nephila pilipes*. The experiments were carried out between March and June in 1999 in a controlled laboratory (temperature: $25 \pm 1^\circ\text{C}$; humidity: 60-90%; light regime: 12 L : 12 D; lights on 0800 h). We collected 24 *Nephila pilipes* juveniles with a body length of 2.0 (± 0.3) cm from Labrador Park. *Nephila pilipes* juveniles were then individually kept in cages (60 \times 60 \times 30 cm) as field observations showed that juvenile webs rarely exceeded 80 cm in diameter. The three sides and top of the cage were covered with wire mesh (mesh size: 3 mm) to allow air circulation, reduce incidence of unwanted prey

entrance and escape of spiders. We then placed a square wooden loop (60 × 60 cm) in the center of the cage to assist in web building for four days and a plastic white board at the bottom of the cage to collect moults. A PVC sheet was used as a front door for the cage to allow easy access to the spiders. We placed two netted cups of water in each cage to continuously provide humidity.

Before the start of the experiment, we weighed each *Nephila pilipes* and put it back to its web. We randomly assigned *N. pilipes* juveniles to four groups, and each group was subjected to the following load of *Argyrodes flavescens*: 0, 2, 4, and 8. *Argyrodes flavescens* were collected from the webs of *N. pilipes* in three study sites. Only adult females of *A. flavescens* (4 mm in body length) were used. No individuals were used more than once in each experiment. In the 30-day experiment, we fed juvenile *N. pilipes* with four houseflies (*Musca domestica* L.) and two mealworms (*Tenebrio molitor* L.) daily. At the end of experiment (30 days after the introduction of *A. flavescens* to the host web), we reweighed each *N. pilipes*, collected moults, monitored mortality, recorded web relocation events, and measured web damage. The weight gain of host spider *N. pilipes* was then calculated as: (final weight - initial weight)/initial weight × 100 %. We determined whether or not the web was relocated by checking if the hub of the new web moved c. 30 cm away from the precedent web. Thus, a removal and rebuilding of the web was counted one relocation. The rate of web relocation was then defined as the mean number of days taken to build a web after removal. We also recorded web dimensions and circular voids in the web caused by both *A. flavescens* and the struggling prey every alternate day. The area of the void is calculated as: πr^2 , where r is the radius of the void. The web damage calculated as a percentage of the void area to the total web area. The mean percentage of web damage per web within 30 days was then calculated.

Statistical analyses

We performed Kolmogorov-Simirov goodness of fit for normality of data to determine whether parametric or non-parametric tests were used (Zar, 1996). Spearman rank correlations were used to examine if the average numbers of *Argyrodes flavescens* found in the host webs were associated with body length of the host spiders, web size, and light intensity. To examine the effects of *A. flavescens* on weight gain, rate of web relocation and web damage, we also performed one-

way ANOVA and post-hoc multi-comparisons. Chi-square test was used to examine the impact of *A. flavescens* on survivorship of *N. pilipes* juveniles. Spearman rank correlations were used to examine the correlations between body length and web area and between web damage and web relocation. All statistic tests are two tailed and significant level is set at 0.05 (Zar, 1996).

RESULTS

Field survey

A total of 196 *Argyrodes flavescens* were found in 34 (69.4%) out of 49 webs of *Nephila pilipes* juveniles and adult females in three study sites (Fig. 1). The maximum number of *A. flavescens* found in the host web was 30; the majority of webs (27 out of 49) contained 1 - 6 *A. flavescens*, with an average of 4.0 ± 0.9 (mean \pm SE) *A. flavescens* per host web. No more than five adult *A. flavescens* were found in a single web of juvenile *N. pilipes* (body length \leq 2 cm) in three study sites.

The mean number of *Argyrodes flavescens* per *Nephila pilipes* web was positively correlated with body length of *N. pilipes* ($r_s = 0.761$, $N = 35$, $p < 0.001$; Fig. 2A), web area ($r_s = 0.337$, $N = 35$, $p < 0.05$; Fig. 2B), and light intensity ($r_s = 0.492$, $N = 34$, $p < 0.01$; Fig. 2C): larger *N. pilipes* and larger web hosted more *A. flavescens* as larger spiders built larger webs ($r_s = 0.562$, $N = 35$, $p < 0.001$; Fig. 3). Webs built in brighter area also hosted more kleptoparasites (Fig. 2C).

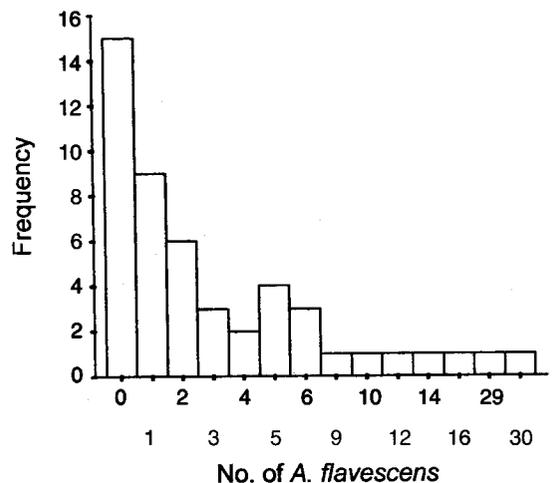


Fig. 1. Frequency of *Argyrodes flavescens* kleptoparasite load per *Nephila pilipes* web recorded in nature.

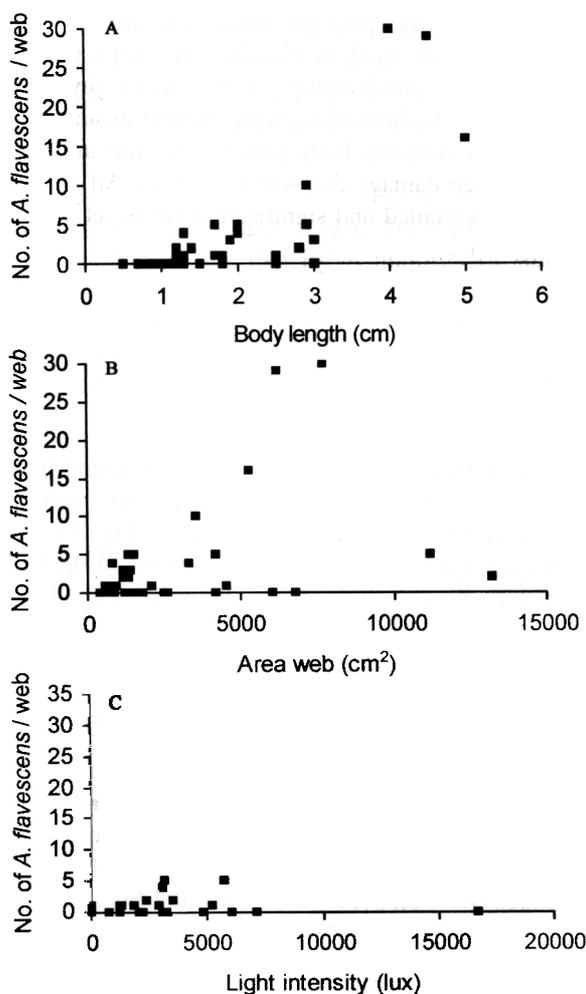


Fig. 2. The correlations between the numbers of *Argyrodes flavescens* per *Nephila pilipes* web and (A) host body length (cm), (B) web area (cm²) of *Nephila pilipes*, and (C) light intensity (lux) around web correlation between body length and web area of *Nephila pilipes*.

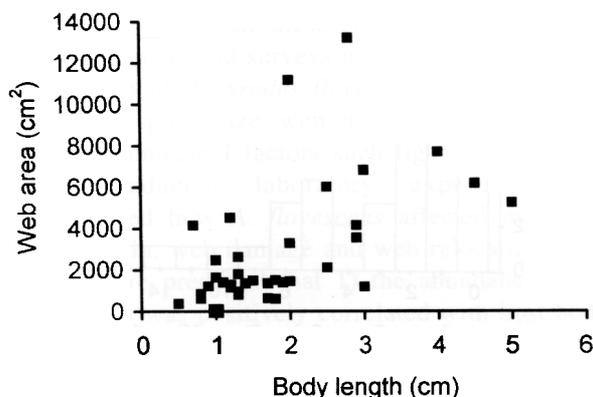


Fig. 3. The correlation between body length (cm) and web area (cm²) of *Nephila pilipes*.

Foraging behaviour of *Argyrodes flavescens*

In the cages (60 × 60 × 60 cm), *Argyrodes flavescens* carefully walks into the web of host spider in c. 30 min after introduction. It often hangs at rest by stretching all its legs at the edge of the web between frame threads. *Argyrodes flavescens* lays down a few fine threads connecting it to several radii of the host's web. In doing so, *A. flavescens* can sense the vibrations in the web generated either by prey or *N. pilipes*. When live *Drosophila melanogaster* lands on the web and generates vibration, it is often ignored by *N. pilipes*. However, *A. flavescens* will approach the small prey by tapping its forelegs. Immediately after locating the prey, *A. flavescens* bites the prey, wraps it, and carries it away from the attacking sites to the edge of web. The wrapped prey by *A. flavescens* is fed upon immediately without further storage. When a housefly hits the web, *Nephila pilipes* immediately moves very fast toward to the struggling prey, attacks, and wraps it. After wrapping the prey, *N. pilipes* carries it back to or near the hub, and

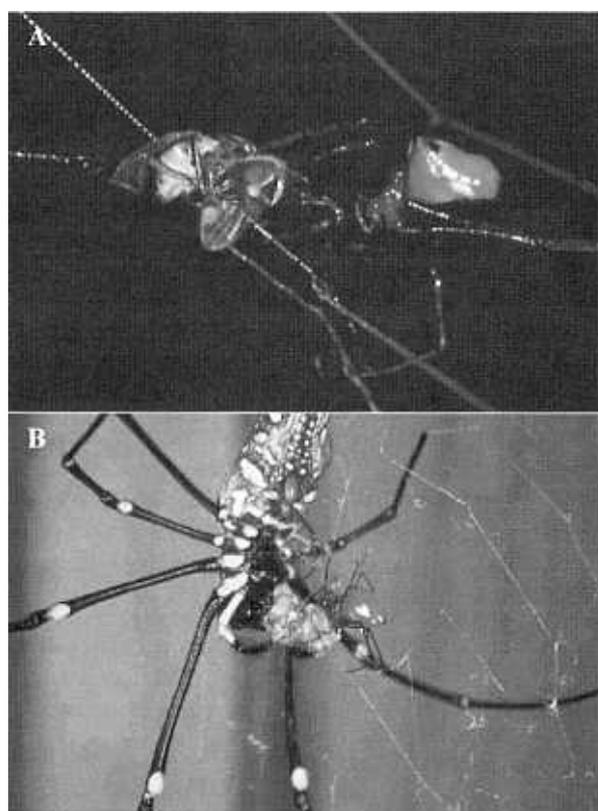


Fig. 4. (A) Female *Argyrodes flavescens* (right; upside down and facing left) stealing a housefly (left) wrapped by *Nephila pilipes*; and (B) Female (far left; upside down and facing left) and male (left; just next to female *A. flavescens*; facing down) *Argyrodes flavescens* sharing a mealworm larva with female *Nephila pilipes*, which is mating with a male (upper; on the ventral side of female *N. pilipes*).

leaves for another attack. *A. flavescens* immediately moves toward the stored housefly, attaches securing threads onto it, cuts the threads connecting the prey item of host web, and carries it away from the host's hub to feed immediately or stores it outside the capture area (Fig. 4A). When *N. pilipes* is attacking and feeding a live mealworm larva (body length: c. 2 cm), *A. flavescens* sometimes shares the food with the host spider (Fig. 4B). *Argyrodes flavescens* also steals the silk from host's web (Fig. 5A), creating voids in the webs and thus generating holes (Fig. 5B).

Laboratory experiments

There was no significant effect of *Argyrodes flavescens* load on survivorship of *Nephila pilipes* juveniles (Chi-square test: $\chi^2 = 6.00$, $df = 3$, NS). However, in the presence of eight *A. flavescens*, 50% of *N. pilipes* juveniles died, and the individuals survived did not moult during the experiments. When no more than four *A. flavescens* were present, all *N. pilipes* juveniles moulted at least once and survived until the end of experiment.

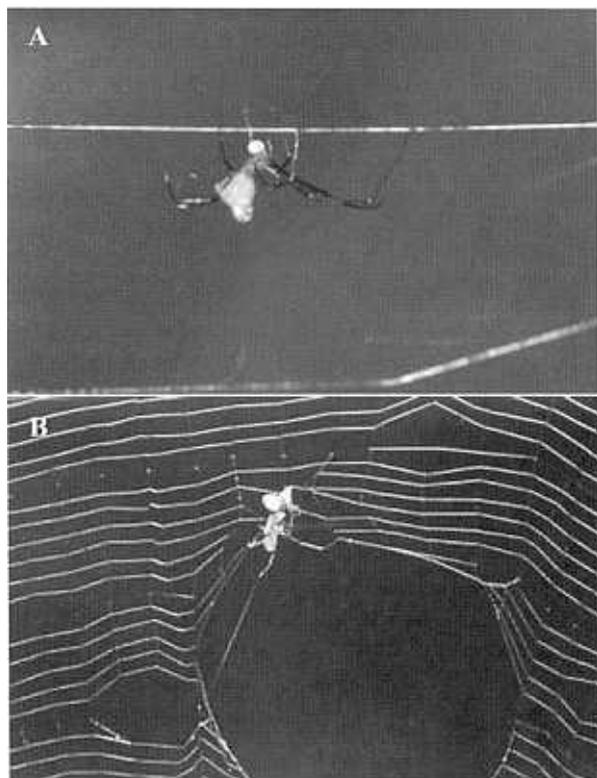


Fig. 5. (A) Female *Argyrodes flavescens* (lower; facing right) with a small silk ball (white) in her mouth hanging on a silk thread; and (B) Female *Argyrodes flavescens* (lower; facing right) feeding on a housefly (upper) stolen from the hub, and web damaged (a large circular void) by prey-stealing action.

The *Argyrodes flavescens* load had significant effect on web damage (ANOVA: $F_{3, 20} = 89.726$, $p < 0.001$): the web damage (%) increased with increasing *A. flavescens* load. Multiple comparisons show that a significant difference in web damage was found for each paired-comparison (see Fig. 6A).

The mean rate of web relocation of *N. pilipes* also significantly increased as *A. flavescens* load increased (ANOVA: $F_{3, 20} = 53.296$, $p < 0.001$) and a significant difference in the rate of web relocation was found for each comparison (see Fig. 6B). The increase in web relocation is correlated to the increase in web damage ($r_s = 0.831$, $N = 24$, $p < 0.001$).

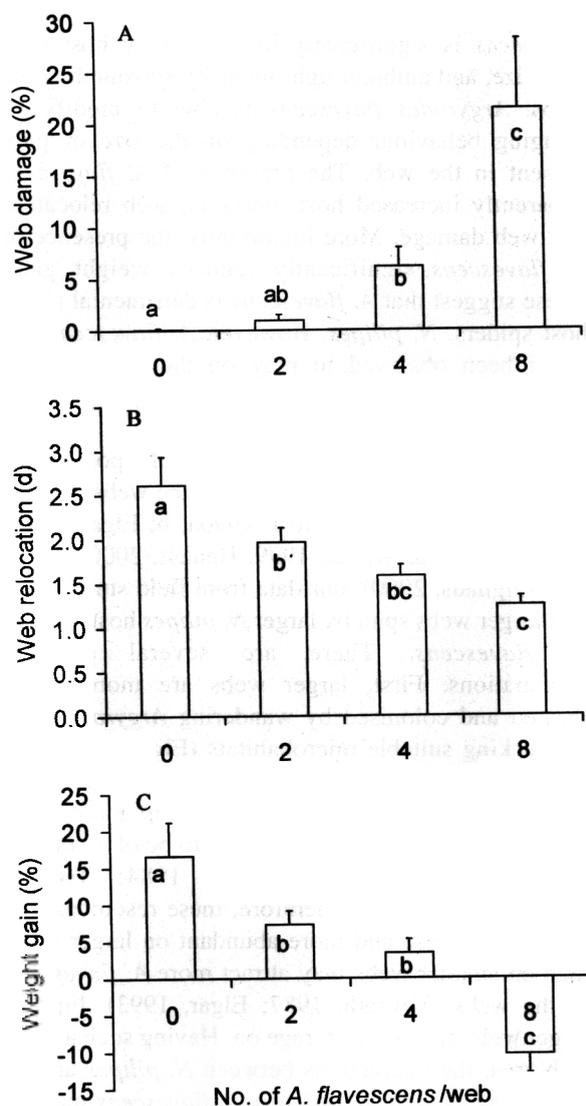


Fig. 6. Effect of *Argyrodes flavescens* load on (A) percentage web damage, (B) rate of web relocation, and (C) weight change of *Nephila pilipes*. Bars marked with different letters are significantly different (Tukey post-hoc: $p < 0.05$).

The presence of *Argyrodes flavescens* had a significant effect on weight gain of *Nephila pilipes* (ANOVA: $F_{3, 18} = 230.3$, $p < 0.01$). Without *A. flavescens*, *N. pilipes* increased its weight by $16.5 \pm 1.9\%$ over the period of study (30 d) but had a weight loss by $10.4 \pm 1.0\%$ when eight kleptoparasites were present on host webs (Fig. 6C).

DISCUSSION

This is the first detailed study of behavioural interactions between kleptoparasitic spiders, *Argyrodes flavescens* and its common host spiders, *Nephila pilipes*, from Singapore. Our study demonstrates that the natural population of *A. flavescens* is significantly influenced by host size, web size, and ambient light intensity surrounding the webs. *Argyrodes flavescens* is able to modify its foraging behaviour depending on the size of prey present in the web. The presence of *A. flavescens* apparently increased host mortality, web relocation and web damage. More importantly, the presence of *A. flavescens* significantly reduced weight gain. These suggest that *A. flavescens* is detrimental to the host spiders, *N. pilipes*. However, *A. flavescens* has never been observed to prey on the host spiders, juveniles or eggs.

Consistent with many studies of population characteristics of kleptoparasites on the webs of web-weaving spiders (Cangialosi, 1990a, b; Elgar, 1989; 1994; Grostal & Walter, 1999; Henaut, 2000; Tso & Severinghaus, 2000), our data from field study show that larger webs spun by larger *N. pilipes* hosted more *A. flavescens*. There are several possible explanations. First, larger webs are more easily located and colonised by wandering *Argyrodes* that are seeking suitable microhabitats (Elgar, 1989; Tso & Severinghaus, 2000). Second, as spiders grow, the webs become larger, hence easily trap more prey, including the ones that are deemed to be of no or less value to the host (Vollrath, 1984; Tso & Severinghaus, 2000). Therefore, these resources that are more diverse and more abundant on larger webs than on smaller webs may attract more *A. flavescens* to the webs (Vollrath, 1987; Elgar, 1993). Finally, larger webs are easy to forage on. Having such a large web area, the interactions between *N. pilipes* and *A. flavescens* as well as between *A. flavescens* may be reduced. Consequently, more *A. flavescens* could reside with little problems with a larger host (Elgar, 1993). In fact, *A. flavescens* was rarely chased by *N. pilipes* on the large webs in the field and even in the cages.

Other factors such as abiotic environmental conditions are also known to influence host-kleptoparasite interactions. In this study, we found that a positive correlation exists between light intensity and the number of *A. flavescens*: the webs in lit sites were significantly invaded by more *A. flavescens*. Recent studies show that web-weaving spiders can recognize the quality of foraging sites or patches and choose web sites on the basis of prey availability (Gillespie & Caraco, 1987). They may also relocate their webs patches with low prey densities to patches with high prey densities (Riechert & Gillespie, 1986). Heiling (1999) showed that the nocturnal orb-web spider *Larinioides sclopetarius* actively chooses lit sites for web construction because these lit sites may have more potential prey, and insect activity is greater in lit sites than unlit sites. Similarly, Adams (2000) found that another species of nocturnal orb-web spider, *Neoscona crucifera*, shows preferences for lit areas where prey densities are high. In this study, webs of *N. pilipes* in brighter areas hosted more *A. flavescens* probably because more insects fly past in the lit sites and thus webs built in these habitats may intercept more insects. Therefore, the webs that can supply sufficient prey may attract more *A. flavescens*. However, the relationship between the abundance of *A. flavescens* and prey density in the lit habitats and in the unlit habitats needs to be studied.

Results from our laboratory experiments demonstrate significant effects of *A. flavescens* on web relocation of host spider, *N. pilipes*. Similar results were reported for the association of *N. plumipes* with *A. antipodianus* from Australia (Grostal & Walter, 1997). The high rate of web relocation in *N. pilipes* may result from the cumulative effects of *A. flavescens* on host feeding, host stress, and prey availability. The web relocation became more frequent as the load of kleptoparasites increased probably due to the lack of food by kleptoparasitism. Rypstra (1981) reported the same result in *Nephila clavipes*: webs are relocated when the number of kleptoparasites increases. Rypstra (1985) and Grostal & Walter (1997) indicated that *Nephila* spiders relocate webs more often when hungry and also when food intake levels start to fall. This reaction in the wild is essential for survival and might be a signal to prevent overcrowding.

Larcher & Wise (1985) also provided evidence that hosts are more likely to abandon webs when *Argyrodes* are present than when absent. The moderate food intake that signals a possible moving in advance helps a spider to survive by providing sufficient energy to construct a web in the new location. Vollrath (1979) noted that in the wild kleptoparasite load is an

indicator of web relocation as *Nephila* leaves web site as a response to high number of *Argyrodes*, thus relocating webs may dramatically reduce the number of kleptoparasites in its new web (Robinson & Robinson, 1976). Spiders have shown to cling on to "successful" sites (Rypstra, 1981) as a spider relocates its web only when the web is damaged severely by the struggling prey after nearly three days. This is to maximize foraging efficiency and possible long-term survival. Furthermore, by relocating *N. pilipes* may force parasites to find a new host, thus significantly reducing the numbers due to predation, as *Argyrodes* spiders are not cryptic (Vollrath, 1979). However, frequent web relocation may cause loss of energy invested in silk and stored prey and may incur a higher risk of predation (Rypstra, 1981; Vollrath, 1985). Although Grostal & Walter (1997) stated that starved spiders are least likely to relocate, while spiders with intermediate food levels are most likely to relocate. Therefore, *Argyrodes flavescens* may steal sufficient food to cause intermediate hunger levels and trigger web relocation but not enough to cause starvation.

Despite this, web relocation rate may be independent of food levels (Vollrath, 1985). Larcher & Wise (1985) demonstrated that, in the presence of *Argyrodes trigonum*, additional food does not prevent hosts from relocating their webs. Alternatively, web relocation may be driven by web damage cause by *Argyrodes*' silk stealing (Tso & Severinghaus, 1998). The spiders have to relocate their webs because the removal of large amount of silk by *A. flavescens* may be disadvantageous to *N. pilipes* through expense of time and energy in reconstructing webs (Grostal & Walter, 1997). In addition, web damage caused by kleptoparasites' silk stealing may also either decrease prey-capture rate by reducing the orb surface area or by allowing insects to fly through the 'holes'. Furthermore, there may be less entanglement between prey and fibres as most of them are digested. Therefore, this may indirectly result in less tension of the web, thus allowing greater escape of prey. This loss in additional protein will then affect the growth of host, thus the host may develop more slowly.

To our knowledge, this is the study experimental study to demonstrate that heavy kleptoparasites increase host mortality: with eight *Argyrodes flavescens* present on the host webs, the caged *Nephila pilipes* suffered 50% mortality at the end of experiments. The increased mortality is probably because *A. flavescens* steals prey items, which would otherwise be eaten by *N. pilipes*. This may result in low energy intake of *N. pilipes*. However, whether this occurs in nature is still not known. In nature, *N. pilipes* can and routinely emigrate

in response to the level of prey consumption, which may otherwise determine the type of interaction between the host and the kleptoparasites. Therefore, whether kleptoparasites increase host mortality in nature needs to be directly clarified.

This study also further confirms the impact of *Argyrodes* spp. on *Nephila* spp. by the experimental evidence that the presence of *A. flavescens* significantly reduced weight gain of host spider *N. pilipes*. This is also supported by the evidence that there was a higher weight gain followed by moulting in the absence of the kleptoparasites. In *N. pilipes*, sufficient food is required for growth especially when they are juveniles. The loss of weight of *N. pilipes* may be due to the reduced food availability as *A. flavescens* removed the captured houseflies directly from the web, which would otherwise be eaten by the host. In addition, *A. flavescens* often approached to the mealworm-feeding *N. pilipes* in the hub and also shared the mealworms with host spiders. Such actions may have a great effect on the host energy budget because the host uses energy, silk and venom to capture prey. A heavier *A. flavescens* load means a higher nutritional requirement. Furthermore, because of the silk consumed by *A. flavescens* in addition to scarcity of food, *A. flavescens* may directly reduce the energy reserves of *N. pilipes*, thus causing weight loss. This reduction in weight gain presents a longer time required to reach maturity, which is supported by a higher rate of moulting of *N. pilipes* in the absence of *A. flavescens*. However, further analyses of wrapped prey that are removed by *A. flavescens* from hosts receiving different kleptoparasitic load will help directly assess the kleptoparasitic relationship between *N. pilipes* and *A. flavescens*.

ACKNOWLEDGEMENTS

This work was supported by grants (R-154-000-060-112 and R-154-000-072-112) to DLi from National University of Singapore. We thank Naomi Diplock, Wee Khee Seah, Lek Min Lim, I-Min Tso and an anonymous referee for their comments on the manuscript. We also thank Singapore National Parks Board for the permit (NP/RP102).

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