



Silk stealing by *Argyrodes lanyuensis* (Araneae: Theridiidae): a unique form of kleptoparasitism

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ABSTRACT

In this study we used field surveys and experiments to investigate silk stealing, a unique form of kleptoparasitism. We studied the role that silk stealing plays in the interactions between a kleptoparasitic spider *Argyrodes lanyuensis* and its giant wood spider host *Nephila maculata* by testing: (1) if silk stealing generates any cost to the hosts; (2) if the amount of web lost to kleptoparasites varies with the size of the host; and (3) how prey stealing by *A. lanyuensis* affects *N. maculata*. Compared with uninhabited webs, *N. maculata* webs invaded by *A. lanyuensis* suffered an average orb reduction of 21%. There was a significant negative correlation between the percentage web reduction and body length of *N. maculata*, indicating that the impact of silk stealing was greater on younger hosts. No significant correlation was found between the number of *A. lanyuensis* on orbs and orb loss, but there was a significant negative relationship between percentage orb loss and silk diameter of *N. maculata*. These results suggest that the finer silk of smaller hosts may be at least partially responsible for their higher percentage orb loss. While prey stealing by other *Argyrodes* species greatly affects the foraging gain of hosts, *A. lanyuensis* did not seem to affect *N. maculata*. This was because the host took larger prey than the kleptoparasite did, and less than 3% of the host's biomass intake came from prey that *A. lanyuensis* would steal.

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Kleptoparasitism is a form of direct competition in which organisms steal food from other organisms, both conspecifics and members of distantly related taxa (Brockmann & Barnard 1979). Although various forms of food stealing are widely observed among mammals and birds, kleptoparasitism is often one of several alternative foraging strategies employed by those organisms. However, in some arthropods food stealing has become the only foraging strategy, and many kleptoparasites are morphologically and behaviourally adapted for this form of foraging. Spiders of the genus *Argyrodes* (Araneae: Theridiidae) are one example.

The majority of species in this genus specialize in stealing prey from various species of spider hosts (Exline & Levi 1962). The long walking legs and highly sensitive vibration sensory organs enable *Argyrodes* spiders to move on hosts' webs without being noticed by the host and to detect the position of trapped prey (Vollrath 1979a; Foelix 1982). Previous studies have demonstrated that various species of *Argyrodes* have four foraging

modes: (1) collecting tiny prey from webs of host spiders (Exline & Levi 1962; Liao et al. 1984); (2) sharing with the host the prey intercepted by webs (Vollrath 1979b); (3) stealing prey from hosts (Vollrath 1979b; Rypstra 1981; Cangialosi 1991); and (4) attacking and consuming host spiders (Smith Trail 1981; Larcher & Wise 1985). In addition to these foraging modes, in our recent field study on Orchid Island, Taiwan, we discovered another little-known form of kleptoparasitism: silk stealing.

Silk stealing has been described in two South American *Argyrodes* species, but very little is known about this unique form of kleptoparasitism. *Argyrodes caudatus* had been seen to consume the supporting strands of small araneid webs, and *A. elevatus* was observed taking down and consuming catching webs of *Nephila* spiders (see Vollrath 1987). However, how silk stealing affects host spiders, and the role silk stealing plays in the foraging of *Argyrodes*, have not been studied further. Recently, we discovered on Orchid Island, Taiwan, a South Asian *Argyrodes* species that takes down and ingests silk from webs spun by giant wood spiders, *Nephila maculata*. This *Argyrodes*–*Nephila* system enabled us to investigate the role silk stealing plays in this kleptoparasite–host interaction. We asked the following questions. (1) Does silk

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stealing by *A. lanyuensis* generate any cost to *N. maculata*? (2) Does the magnitude of silk stealing vary between *N. maculata* individuals of different size? (3) Compared with silk stealing, how does prey stealing by *A. lanyuensis* affect foraging by *N. maculata*?

METHODS

Study Site and Spiders

We conducted the study between 11 and 15 May and 18 and 20 June 1997, on Orchid Island (Lanyu in Chinese, 22°N, 121.5°E), a tropical volcanic island 91 km off the southeast coast of Taiwan. Orchid Island's climate is characterized by high temperatures (average 22.4°C), high precipitation (more than 2600 mm per year) and high relative humidity (more than 90%). The study site (under the 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. Giant wood spiders, *Nephila maculata* Fabricius 1793 (Araneae, Tetragnathidae), of all developmental stages were abundant in the study site. The body length of a mature female may reach 35–50 mm and the orb radius may reach 1.5 m (I. M. Tso & L. L. Severinghaus, personal observations). Males (about 10 mm long) can sometimes be seen on females' webs guarding their mate. *Argyrodes lanyuensis* sp. nov. (Yoshida et al., in press), a previously undescribed, small, silvery spider with slender, dark-brown appendages (adult body size 3–4 mm), can frequently be found on the edge of orbs or in the barrier webs of *N. maculata*. Although other *Nephila* spiders are reported to be able to shorten the time they are away from the hub to reduce food stealing (Vollrath 1979b), *N. maculata* seemed to pay no attention to ongoing silk stealing.

Effect of *A. lanyuensis* on Orb Loss of Host

During our May field trip, we marked web sites of 31 *N. maculata* by fastening plastic strips in the vegetation nearby. We also marked spiders by applying enamel paint on the dorsal surface of the abdomen. During the study we visited each web site five times each day between 0800 and 1800 hours. In the first survey of the day we recorded the body length of *N. maculata*, the orb area and number of *A. lanyuensis* on the orbs. In the last survey of the day we estimated orb area again. In addition, during each visit we recorded the number, size and position of *A. lanyuensis* on orbs. To ensure that the orb loss recorded resulted from silk stealing by kleptoparasites rather than from damage caused by prey, we monitored the position of *A. lanyuensis* and the damage they caused on orbs five times a day. In the last survey of the day, in the majority of invaded webs, *A. lanyuensis* could still be seen consuming silk at the recorded spot. We applied enamel paint in the centre and to eight cardinal points on the edge of the hub to ensure that we measured the identical orb radius in the first and last survey of the day. Because the orbs spun by *N. maculata* were vertically asymmetric, we used a formula provided by M. E. Herberstein (personal

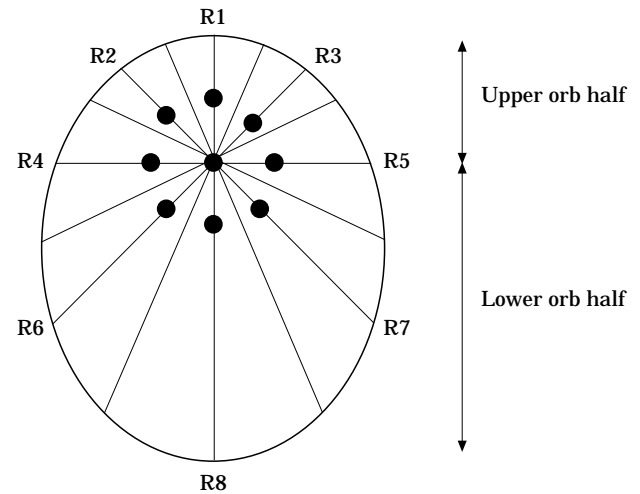


Figure 1. A schematic diagram of the vertically asymmetric orb spun by *Nephila maculata* demonstrating how orb area was estimated. Enamel paint (●) was applied in the centre and to eight cardinal points of the hub to ensure that the identical orb radius was measured in different surveys. The formula used in estimating the orb area is as follows: Orb area=area of upper orb half+area of lower orb half

$$= \frac{1}{2} \pi \left[\frac{(R_1 + R_2 + R_3 + R_4 + R_5)}{5} \right]^2 + \frac{1}{2} \pi \left[\frac{(R_4 + R_5 + R_6 + R_7 + R_8)}{5} \right]^2$$

The formula used in the field experiment estimating the area of orb half (left orb half as example) is as follows: Left orb half area=area of upper left half+area of lower left half

$$= \frac{1}{4} \pi \left[\frac{(R_1 + R_2 + R_4)}{3} \right]^2 + \frac{1}{4} \pi \left[\frac{(R_4 + R_6 + R_8)}{3} \right]^2$$

communication) to estimate the orb area (see Fig. 1). According to pre-experiment surveys, most silk stealing occurred at the edge of the orb, and shortened some of the orb radii measured. By comparing the area estimated from the average radius of eight cardinal points before and after the actions of *A. lanyuensis*, we could quantify the reduction in orb size. The estimated reduction in orb size of each *N. maculata* was then divided by the orb size recorded from the first survey to generate a percentage reduction in orb size. We assessed the effect of *A. lanyuensis* on *N. maculata* by comparing with a Mann–Whitney *U* test the percentage reduction in orb size between invaded and uninvaded webs. To evaluate if web reduction caused by *A. lanyuensis* varied between hosts of various sizes, we performed a Spearman correlation between percentage orb reduction and body length of *N. maculata*. We conducted another Spearman correlation to assess if the number of *A. lanyuensis* correlated with the amount of orb reduction. Because the number of *A. lanyuensis* on a given web of *N. maculata* may have varied from survey to survey, we used the mean from five surveys of the day to perform the correlation.

Field Experiment

To control for factors that also result in orb loss, such as silk diameter and environmental variables (wind, fallen leaves, etc.), we conducted a field experiment by manipulating the presence of *A. lanyuensis* between two halves of an orb. Between 18 and 21 June, we marked and randomly divided 29 *N. maculata* webs into two groups: control and experimental. In the control group we removed all *A. lanyuensis* from both halves of the hosts' orbs. In the experimental group we removed *A. lanyuensis* from either the left or right half of the orb but those on the other half were allowed to stay. We monitored orbs from both control and experimental groups hourly to maintain the treatment. Area and percentage reduction of both halves of webs of the control and experimental groups were estimated with the formula given in Fig. 1. A Wilcoxon signed-ranks test was used to compare the percentage reduction of invaded and uninvaded halves of the orb in the experimental group, and left and right halves in the control group. Since this test compares the area loss of two halves of an orb, compounding variables associated with web characteristic and location can be controlled.

Host Spider Silk Collection and Diameter Estimation

In the field we always observed *A. lanyuensis* teasing a fine filament from a host's silk thread, rolling it into a small ball, then ingesting it. This phenomenon suggests that the number of filaments in a silk thread, which correlates with the diameter of the silk, may affect the amount of orb loss from silk stealing. To investigate if silk diameter is responsible for any variation in orb loss among *N. maculata* individuals of different sizes, we measured body length and collected orb silk from 21 female *N. maculata* (body size 8–45 mm) during the June field trip. We collected an area of 9×2.5 cm between the hub and the lowest spiral with frames made from transparent film and carried back the collected silk to our laboratories in the Institute of Zoology, Academia Sinica, Taiwan for measurement. To collect silk, we applied clear glue to one side of the frame, pressed the frame on to the web then burned the silk around the frame to free it from the web. Silk diameter was estimated (under $1000\times$) by a micrometer fitted on a Nikon Optiphot compound microscope. We made five measurements of both the radii and spiral, and a mean derived from those 10 readings was used in the statistical analysis. Since the silk diameter estimated from the 21 *N. maculata* was normally distributed (Lilliefors test: $P > 0.05$), we conducted a linear regression to examine the relationship between silk diameter and body length. In addition, we also conducted a linear regression between percentage reduction of invaded orb halves and their silk diameter to see if a negative relationship could be found between those two variables.

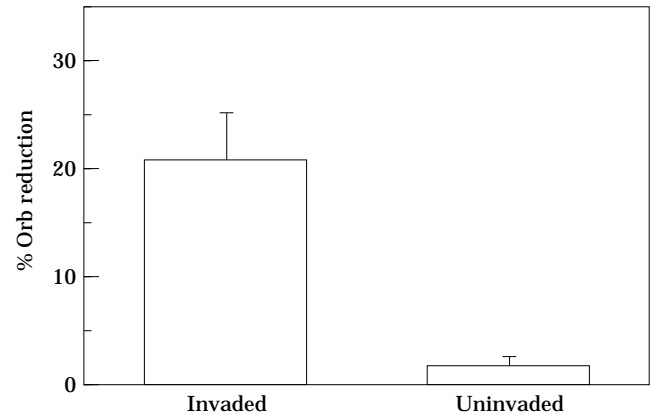


Figure 2. Percentage orb reduction ($\bar{X} \pm SE$) of *Argyrodes lanyuensis*-invaded and uninvaded webs spun by *Nephila maculata*.

Effect of *A. lanyuensis* on Prey Consumption of Host

We recorded the taxonomic order and size of prey consumed by *N. maculata* and *A. lanyuensis* hourly in both the May and June field trips. To examine if the prey consumed by the host and kleptoparasites overlapped in size, we performed a Kolmogorov–Smirnov test to compare their prey size distributions. In addition, we also estimated the dry weight of recorded prey using the length–weight regression equations provided by Schoener (1980) to determine the host spiders' biomass intake from various size categories of prey. This was to evaluate if prey that could potentially be stolen by *A. lanyuensis* represented a significant part of the total prey biomass intake of the host.

RESULTS

Effect of *A. lanyuensis* on Orb Loss of Host

From 2 days of monitoring in May, we recorded 31 cases of orb reduction. Among them 22 were from *A. lanyuensis*-invaded and nine from uninvaded webs. Invaded webs of *N. maculata* suffered a significantly higher percentage of web reduction than did uninvaded webs (Mann–Whitney U test: $U = 173.500$, $N_1 = 22$, $N_2 = 9$, $P < 0.001$; Fig. 2). The field manipulation experiment conducted in June generated similar results (Fig. 3). Owing to severe weather, complete data were recorded from only 13 spiders. In the experimental group, a significant percentage of orb reduction was found in invaded halves (Wilcoxon signed-ranks test: $Z = -2.380$, $N = 8$, $P < 0.05$; Fig. 3a) compared with uninvaded halves. In the control group, no significant difference in percentage orb reduction was found between left and right halves of the orb ($Z = -1.609$, $N = 5$, NS; Fig. 3b).

Variation in Percentage Orb Reduction

The percentage orb reduction was negatively correlated with the body length of *N. maculata* ($r_s = -0.444$, $N = 22$,

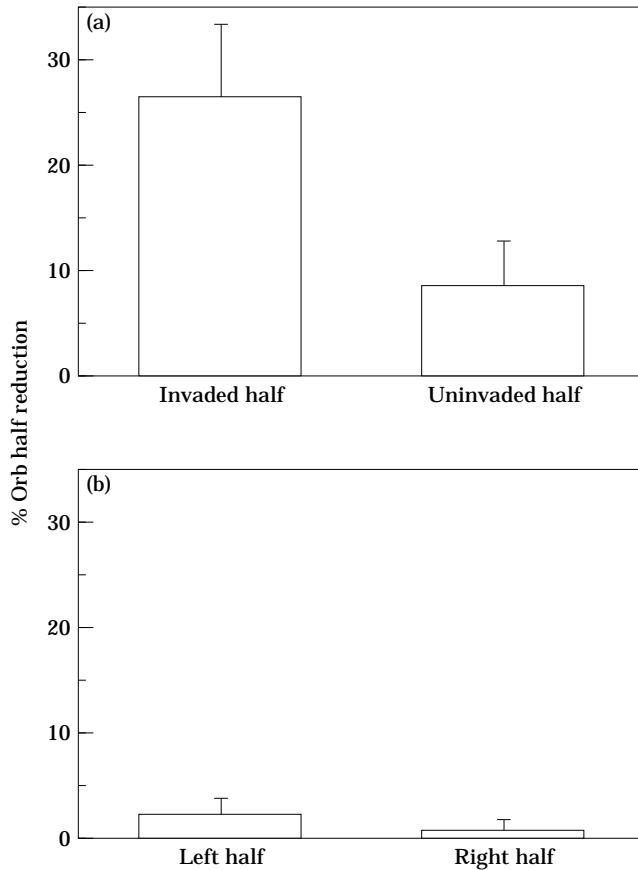


Figure 3. Percentage reduction ($\bar{X} \pm \text{SE}$) of orb halves: (a) experimental group with half of each orb invaded by *Argyroides lanyuensis* and half uninvaded; (b) control group with no *A. lanyuensis* on either half.

$P < 0.05$; Fig. 4a). This result suggests that smaller *N. maculata* suffered greater web destruction by the invasion of *A. lanyuensis*. The greater orb reduction in smaller hosts did not seem to result from more *A. lanyuensis* on the orb, because no significant correlation was found between the number of *A. lanyuensis* and percentage orb reduction ($r_s = -0.005$, $N = 22$, NS). Nor was there a significant correlation between orb size of *N. maculata* and average number of *A. lanyuensis* on the orb ($r_s = -0.034$, $N = 22$, NS). A survey conducted on 14 May showed that the average number of *A. lanyuensis* on hosts' webs and percentage of host webs invaded by kleptoparasites varied during the day (Fig. 5). A significant positive relationship was found between silk diameter and body length of 21 *N. maculata* recorded in June, however ($r^2 = 0.884$, $F_{1,19} = 145.062$, $P < 0.01$; Fig. 4b). Moreover, a significant negative relationship was found between percentage orb loss of invaded web halves of eight *N. maculata* in the experimental group and their silk diameter ($r^2 = 0.758$, $F_{1,6} = 18.829$, $P < 0.01$; Fig. 6).

Prey Size Distribution

Combined from both May and June surveys, 55 prey were recorded from *N. maculata* and 28 from *A.*

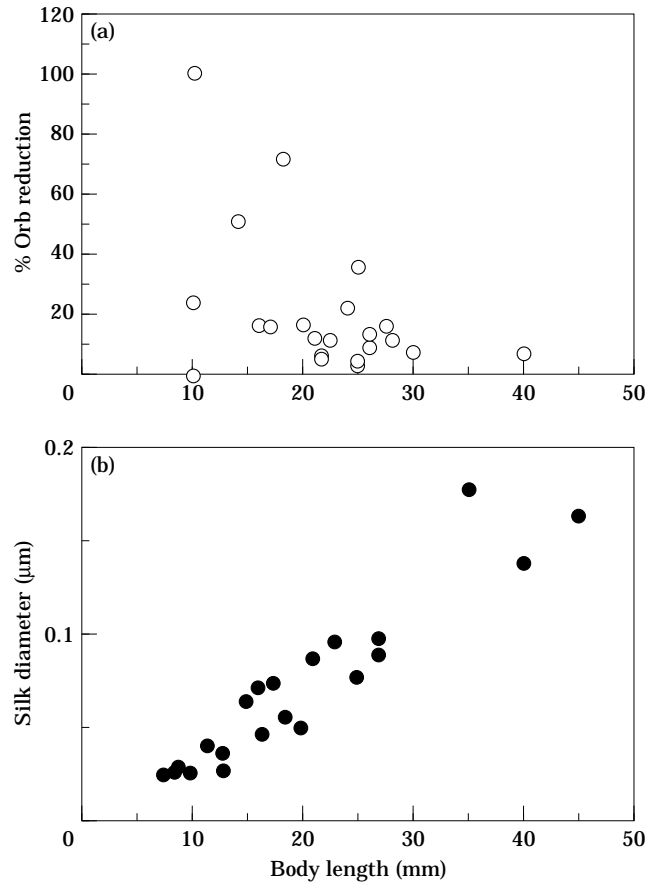


Figure 4. The relationship between (a) percentage orb reduction and body length (in mm) recorded in May from 22 *Argyroides lanyuensis*-invaded webs spun by *Nephila maculata*; and (b) silk diameter (in μm) and body length recorded in June from 21 *N. maculata*.

lanyuensis. There was a significant difference between the prey size distributions of *N. maculata* and *A. lanyuensis* (Kolmogorov–Smirnov statistic = 0.747, $P < 0.01$). The size of prey consumed by the host ranged from 2 to 19.5 mm, but that of *A. lanyuensis* ranged only from 1 to 4 mm. Although prey smaller than 4 mm constituted 18.2% of *N. maculata*'s total prey in number (Fig. 7a), less than 3% of the host's biomass intake came from this size category (Fig. 7b). While other *Argyroides* species have been reported to affect the prey consumption of host spiders, the effect of *A. lanyuensis* on that by *N. maculata* did not seem to be severe.

DISCUSSION

This study demonstrates that *A. lanyuensis* can considerably reduce the orbs of its hosts by silk stealing. Although the average orb reduction caused by *A. lanyuensis* was about 20%, we have seen many *N. maculata* webs losing more than half their orbs to kleptoparasites. The most extreme case we recorded was when two *A. lanyuensis* completely consumed a web spun by *N. maculata* (body length = 10 mm, orb area = 375 cm²) in 8 h. Silk stealing may be costly to host spiders in two ways.

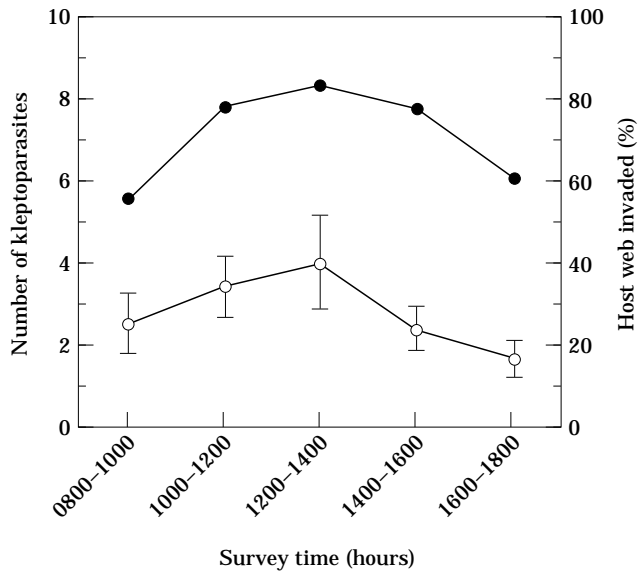


Figure 5. Number ($\bar{X} \pm SE$) of *A. lanyuensis* on webs spun by *Nephila maculata* (○) and percentage of *N. maculata* webs invaded (●) recorded from five surveys.

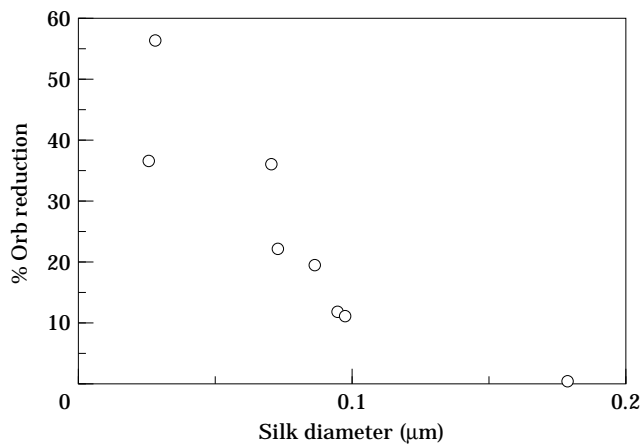


Figure 6. The relationship between orb loss of *A. lanyuensis*-invaded halves of webs spun by eight *N. maculata* in the experimental group and their silk diameter.

First, orb size correlates positively with number of prey intercepted in *Nephila* and other orb-weaving spiders (Chacon & Eberhard 1980; Brown 1981; Craig 1989; Higgins & Buskirk 1992; Herberstein & Elgar 1994). Therefore, a loss of web area may reduce the foraging gain of host spiders. Second, the material spiders invest in web silk represents a considerable portion of a spider's total energy reserves (Prestwich 1977), and most orb weavers remove and ingest silk to conserve this valuable resource (Peakall 1971; Carico 1986; Townley & Tillinghast 1988). Silk consumed by *Argyrodes* directly reduces the energy reserves of the host spiders. Considering the potential reduction in foraging gain and energy reserves caused by web loss, the impact of *A. lanyuensis* on *N. maculata* could be considerable. However, further investigations are needed to evaluate these costs.

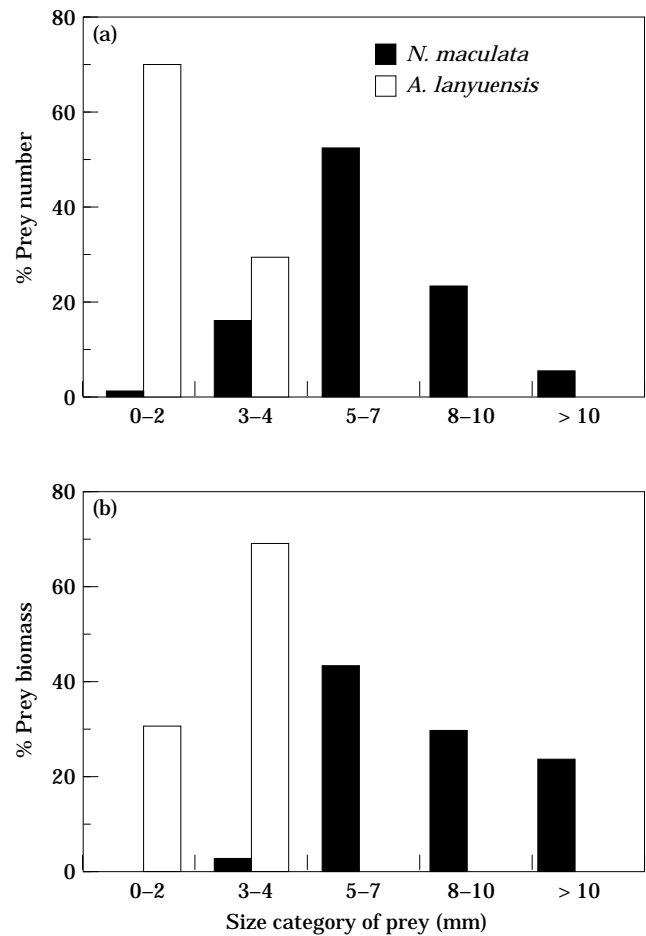


Figure 7. Size distribution of prey consumed by *Argyrodes lanyuensis* ($N=28$) and *Nephila maculata* ($N=55$). (a) Percentage of prey number from each size category. (b) Percentage of prey biomass from each size category.

The magnitude of web reduction caused by *A. lanyuensis* may be greater than that estimated in this study. Although most silk stealing observed occurred at the edge of orbs, we have seen *A. lanyuensis* consume silk from the inner portion of orbs and generate holes. However, we excluded damage in the inner part of orbs from our analysis, because it was difficult to measure. In addition, on several of the webs we monitored, damage caused by silk consumption occurred in the region between the radii measured. Since the designated radius was not altered in these webs, we had to assign the area of these webs as unchanged. Moreover, we did not record silk consumption that occurred in the barrier web, because it was difficult to quantify material loss. However, *A. lanyuensis* wanders freely between the orb and barrier web and consumes silk from both parts of the web. Considering silk loss from all possible sources, the actual costs *A. lanyuensis* generates should exceed the value estimated in this study.

We also demonstrated that silk stealing affects small and large host spiders to different degrees. A significant negative relationship was found between body length of

hosts and percentage web reduction. Because no significant correlation was found between the average number of *A. lanyuensis* on orbs and orb loss, the larger orb loss of smaller *N. maculata* may be due to the finer silk thread produced. Silk thread is composed of strands of filament produced from a number of spigots on the spinnerets. Juvenile spiders have few spigots but gain more as they go through successive moults (Foelix 1982). Therefore, webs of young *N. maculata* were spun of finer silk consisting of fewer filament strands. We frequently observed *A. lanyuensis* teasing a fine filament from a silk thread and rolling it into a small ball before ingestion. Larger *N. maculata* are able to produce silk threads containing more filaments and the consumption of this silk by *A. lanyuensis* may only reduce thread diameter without breaking it, and thus damages little of the web area. However, the same amount of foraging on finer silk may result in the silk being completely ingested, and the consequent disappearance of a whole sector of a web.

The number of *Argyrodes* was previously reported to correlate positively with colony size of a social host (Cangialosi 1990) or solitary host (Elgar 1989), and was correlated with the web volume of solitary hosts (I. M. Tso, unpublished data). However, in our study no significant correlation was found between orb area of *N. maculata* and average number of *A. lanyuensis* on the orbs. This lack of correlation may be a result of *A. lanyuensis*'s frequent movements on and off the orb, because the average number of *A. lanyuensis* on host webs and the percentage of host webs invaded by *A. lanyuensis* varied during the day (Fig. 5). Whitehouse & Jackson (1993) reported that the number of *A. antipodiana* on host webs varied from day to day, but our results indicate that densities of *Argyrodes* may even oscillate on an hourly basis. In addition to the individuals on hosts' webs, there seemed to be a population of *Argyrodes* wandering in the vegetation searching for suitable host webs to invade.

Larcher & Wise (1985) suggested that host/*Argyrodes* size ratios greatly determine the outcome of kleptoparasitic interactions, and this seems also to occur in *Nephila*-*Argyrodes* systems. For example, the majority of prey consumed by *Nephila clavipes* (adult body length around 20 mm) recorded by Rypstra (1981) were smaller than 5 mm, which overlaps considerably with prey consumed by the kleptoparasitic *Argyrodes*. In this host-kleptoparasite system, *N. clavipes* lost a considerable amount of prey to *Argyrodes* sp. However, in our study more than 80% of prey consumed by *N. maculata* of various sizes were larger than 4 mm (Fig. 7a), and more than 97% of biomass came from prey larger than 4 mm (Fig. 7b). Therefore, the impact of prey stealing by *Argyrodes* seems to be inversely proportional to the size of *Nephila* hosts.

Argyrodes lanyuensis seems to rely on different forms of energy at various developmental stages. Although both large individuals (body length > 3 mm) and juveniles consumed silk from webs of hosts, 70% of the prey we recorded being consumed came from large *A. lanyuensis*. Vollrath (1984) suggested that early instar *Argyrodes* live

exclusively on silk. In this study we did not estimate the time budgets of large and small *A. lanyuensis* regarding these two energy-acquiring strategies. Perhaps silk consumption is the major foraging mode for early instar *A. lanyuensis*, and prey consumption becomes more and more dominant as it goes through successive moults. Further investigation of the role that the two foraging modes play in different life stages of *A. lanyuensis* is needed to understand if their impact on orb-weaving hosts varies with age.

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References

- Brockman, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. *Animal Behaviour*, **27**, 487–514.
- Brown, K. M. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia*, **50**, 380–385.
- Cangialosi, K. R. 1990. Life cycle and behavior of the kleptoparasitic spider, *Argyrodes ululans* (Araneae, Theridiidae). *Journal of Arachnology*, **18**, 347–358.
- Cangialosi, K. R. 1991. Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. *Animal Behaviour*, **41**, 639–647.
- Carico, J. E. 1986. Web removal patterns in orb-weaving spiders. In *Spiders, Webs, Behavior, and Evolution* (Ed. by W. A. Shear), pp. 306–318. Stanford: Stanford University Press.
- Chacon, P. & Eberhard, W. G. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. *Bulletin of the British Arachnological Society*, **5**, 29–38.
- Craig, C. L. 1989. Alternative foraging modes of orb weaving spiders. *Biotropica*, **21**, 257–264.
- Elgar, M. A. 1989. Kleptoparasitism; a cost of aggregation for an orb-weaving spider. *Animal Behaviour*, **37**, 1052–1055.
- Exline, H. & Levi, H. W. 1962. American spiders of the genus *Argyrodes* (Araneae, Theridiidae). *Bulletin of the Museum of Comparative Zoology, Harvard*, **127**, 75–204.
- Foelix, R. F. 1982. *Biology of Spiders*. Cambridge, Massachusetts: Harvard University Press.
- Herberstein, M. E. & Elgar, M. A. 1994. Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneidae): nocturnal and diurnal orb-weaving spiders. *Australian Journal of Ecology*, **19**, 451–457.
- Higgins, L. E. & Buskirk, R. E. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. *Animal Behaviour*, **44**, 485–499.

- Larcher, S. F. & Wise, D. H. 1985. Experimental studies of the interactions between a web-invading spider and two host species. *Journal of Arachnology*, **13**, 43–59.
- Liao, C., Chen, M. & Song, D. 1984. On morphological characteristics and biology of the silk spider *Nephila imperialis* (Araneae; Araneidae). *Acta Zoologica Sinica*, **30**, 67–71.
- Peakall, D. B. 1971. Conservation of web proteins in the spider *Araneus diadematus*. *Journal of Experimental Zoology*, **176**, 257–264.
- Prestwich, K. N. 1977. The energetics of web-building in spiders. *Comparative Biochemistry and Physiology*, **57**, 321–326.
- Rypstra, A. L. 1981. The effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. *Oikos*, **37**, 179–182.
- Schoener, T. W. 1980. Length–weight regression in tropical and temperate forest-understory insects. *Annals of the Entomological Society of America*, **73**, 106–109.
- Smith Trail, D. 1981. Predation by *Argyrodes* (Theridiidae) on solitary and communal spiders. *Psyche*, **8**, 349–355.
- Townley, M. A. & Tillinghast, E. K. 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, gabamide. *Journal of Arachnology*, **16**, 303–319.
- Vollrath, F. 1979a. Vibrations; their signal function for a spider kleptoparasite. *Science*, **205**, 1149–1151.
- Vollrath, F. 1979b. Behaviour of the kleptoparasitic spider *Argyrodes elevatus* (Araneae, Theridiidae). *Animal Behaviour*, **27**, 515–521.
- Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. In: *Producers and Scroungers* (Ed. by C. J. Barnard), pp. 61–94. Beckenham, Kent: Croom Helm.
- Vollrath, F. 1987. Kleptobiosis in spiders. In: *Ecophysiology of Spiders* (Ed. by W. Nentwig), pp. 274–286. Berlin: Springer-Verlag.
- Whitehouse, M. A. & Jackson, R. R. 1993. Group structure and time budgets of *Argyrodes antipodiana* (Araneae, Theridiidae), a kleptoparasitic spider from New Zealand. *New Zealand Journal of Zoology*, **20**, 201–206.
- Yoshida, H., Tso, I. M. & Severinghaus, L. L. In press. Descriptions of a new species of the genus *Argyrodes* (Araneae: Theridiidae) from Orchid Island, Taiwan, with notes on its ecology and behavior. *Acta Arachnologica*.