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Host selection by a kleptobiotic spider

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Abstract Why do kleptobiotic spiders of the genus *Argyrodes* seem to be associated with spiders of the genus *Nephila* worldwide? Observations following introduction of experimental insect prey of different sizes and weights on to host webs revealed that: (1) small prey are more effectively retained on the web of *Nephila clavipes* than on the web of another common host, *Leucauge venusta*. (2) *N. clavipes* did not consume small prey that accumulated on the web whereas larger, heavier prey were enveloped and stored. (3) We observed clear partitioning of prey items between *N. clavipes* and *Argyrodes* spp.; diet selection by *Argyrodes* did not overlap with that of *N. clavipes* but closely overlapped with that of *L. venusta*. (4) *L. venusta* responds very quickly to prey impact whereas *N. clavipes* is slower, offering a temporal window of opportunity for *Argyrodes* foraging. (5) The ability of *L. venusta* to detect and respond to small items also means that it acts aggressively to *Argyrodes* spp., whereas *N. clavipes* does not. Consequently, food-acquisition behaviours of *Argyrodes* were clearly less risky with *N. clavipes* compared with *L. venusta*. We conclude that when a kleptobiotic organism has a choice of various host species, it will opt for the least risky host that presents the highest rate of availability of food items. The fact that *Nephila* species present such characteristics explains the worldwide association with *Argyrodes* kleptobiotic spiders.

Introduction

Spider webs can be excellent foraging patches, providing a range of food items, including insects caught on the web, host spider progeny, the host spider, and the web itself (Hénaut 2000; Whitehouse et al. 2002). *Argyrodes*, a large cosmopolitan genus of Theridiidae spiders, noted for its kleptobiotic habits on the webs of other spiders (Kullman 1959; Exline and Levi 1962; Vollrath 1979; Larcher and Wise 1985), has to select a host based on foraging opportunities (Cangialosi 1997). However, the presence of the host can be costly to *Argyrodes* (Elgar 1993; Whitehouse 1997).

A strong relationship between *Nephila* spp. spiders and *Argyrodes* has been observed and appears to be cosmopolitan (Rypstra 1981; Whitehouse et al. 2002). We asked whether the apparent preference by *Argyrodes* for *Nephila* webs is due to low predation risk, or high food availability and rate of food acquisition due to little competition from *Nephila*. A new classification (Agnarsson 2004) has introduced a new subfamily, *Argyrodinae*, and the *Argyrodes* species described in this study, *Argyrodes globosus* and *A. caudatus*, have been renamed *Faidatus globosus* and *F. caudatus*. However, this classification has yet to be adopted generally and, for clarity, we have chosen to retain the established genus name *Argyrodes* here.

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Materials and methods

Distribution of *Argyrodes* in coffee plantation

In July 2002, vegetation was manually cleared in an uncultivated cacao (*Theobroma cacao* L.) plantation located 400 m above sea level, at Rosario Izapa, Chiapas, Mexico, which forced *Argyrodes* spp. and *Nephila* spp. to move to an adjacent cultivated coffee (*Coffea arabica* L.) plantation (~1 ha), from which they were formerly absent (Hénaut and Ibarra 2001). To determine the effect of relocation on host selection by *Argyrodes*, the number of *Argyrodes* spp. individuals associated with each spider web in the coffee plantation was counted in September 2002. Only known species of hosts for *Argyrodes* in Chiapas, Mexico, were considered

in this survey (Hénaut 2000). The two principal species of *Argyrodes* (*A. caudatus* and *A. globosus*) are readily distinguished by eye, and individuals were identified when observed on the host web. Specimens of other species were transported to the laboratory and identified by microscopic examination using the keys of Exline and Levi (1962).

Naturally occurring prey on webs

We collected the prey and debris present on the webs of *Nephila clavipes* and *Leucauge venusta* that had not been captured by the spiders. *Leucauge* was chosen over other host species for its abundance. We measured, or estimated when damaged, the length of each prey item from the extreme anterior point of the head to the hindmost part of the abdomen using a binocular microscope.

Behaviour of spiders towards experimental prey

Twelve webs of each host species *N. clavipes* and *L. venusta* were selected, on to which living experimental prey, chosen on the basis of their body length and live weight to represent a range of prey similar to those observed in webs at the study site, were individually introduced by blowing them onto the web, as described previously (Hénaut et al. 2001). Prey comprised *Anopheles pseudopunctipennis* (Culicidae), *Drosophila melanogaster* (Drosophilidae), *Ceratitis capitata* irradiated males (Tephritidae), *Anastrepha ludens* (Tephritidae) and *Apis mellifera* females (Apidae). Ten individuals of each prey (total $N=120$ per prey species) were introduced one after another. Only prey stopped by the web and retained >2 s were considered. When a prey item was not captured, it was observed for a period of 30 min. The interval between introducing one prey item and the next was 5 min. We recorded the number of prey captured and retained on the web but not captured, the time taken by each spider to capture the prey, and the number of prey captured or stolen by *Argyrodes* spp. during the experiment (30 min). The mean weight: size ratio for each prey type was calculated, rather than weight or size alone, as large differences in the shapes of insects could adversely affect the results.

Argyrodes strategies on the *Nephila* web

Ten webs of *N. clavipes* were selected and the behaviour of *Argyrodes globosus* was observed. To ensure that each web contained a large quantity of prey and to stimulate spider activity, ten sterile male fruit flies (*Ceratitis capitata*) were introduced to each web by blowing them. Activity of *Argyrodes* spp. ($N=15$) on the web was observed for 1 h. Behaviour was classified as: (i) glean small insects, (ii) steal a prey item caught by the host, (iii) steal a food bundle caught and processed by the host, (iv) consume a prey item with the host. No distinction was made between experimental and natural prey. Attempts to steal prey items (defined as the oriented approach to a prey item, with or without touching it) were calculated. Log likelihood ratio tests (G -tests) were used to compare the number of insects of each type of prey collected in webs and the number of each type of experimental prey captured. Mann-Whitney test was used to compare the velocity of capture between host species. The procedure was repeated with *Argyrodes caudatus*.

Results

Distribution of *Argyrodes* in coffee plantation

Argyrodes spp. ($N=130$) were only observed in association with *N. clavipes* in the coffee plantation although other *Argyrodes* host species were present, including *L. venusta* ($N=20$), *Gasteracantha cancriformis* ($N=20$), and

Verrucosa arenata ($N=8$). Of the five species of *Argyrodes* found, the two most abundant were *Argyrodes caudatus* ($N=81$, 62% of total) and *Argyrodes globosus* ($N=38$, 29% of total).

Naturally occurring prey on webs

No prey items and no prey remains were observed on the web of *L. venusta*. The prey items observed on the web of *N. clavipes* but not captured were common and consisted of small insects (mean \pm SE, 1.30 ± 0.05 mm, $N=98$), whereas larger prey (8.9 ± 0.9 mm, $N=22$) were enveloped and stored.

Behaviour of spiders towards experimental prey

The distribution of *L. venusta* captures of experimental prey (Fig. 1a) was significantly biased in favour of small prey items ($G_{\text{adj}}=195.6$, $df=4$, $P<0.001$). In contrast, the distribution of *N. clavipes* captures of experimental prey (Fig. 1b) was significantly biased in favour of large prey ($G_{\text{adj}}=76.8$, $df=4$, $P<0.001$). Only a few *Anopheles pseudopunctipennis* (20% of total mosquito prey) were retained for the 30-min period on webs of *L. venusta*. The web of *N. clavipes* retained the smallest insects, although they were not captured by the host (78% of *Anopheles pseudopunctipennis*, 15% of *D. melanogaster*). Response times were rapid in *L. venusta* (mean capture time \pm SE, 7.4 ± 1.1 s), but slower in *N. clavipes* (18.3 ± 1.3 s) (Mann-Whitney $U=9934$, $P<0.001$). *Argyrodes* consumed mainly small, light prey, such as *Anopheles pseudopunctipennis* and *D. melanogaster*, over larger prey ($G_{\text{adj}}=9.9$, $df=2$, $P=0.006$, Fig. 1c).

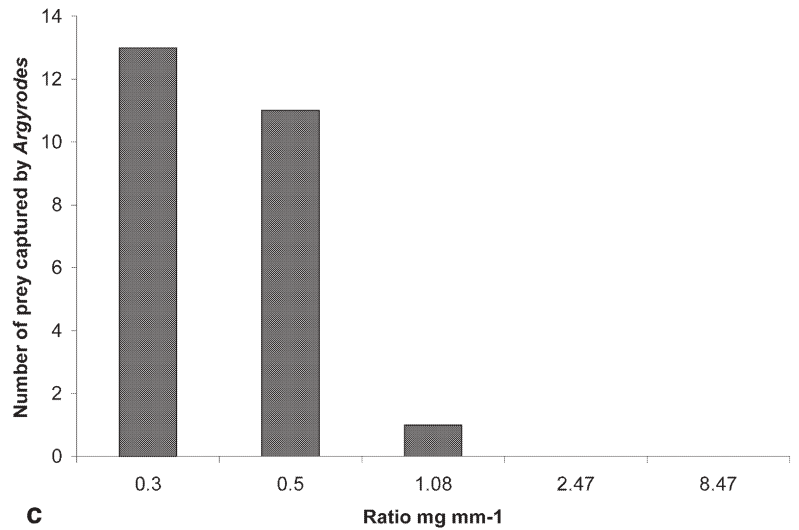
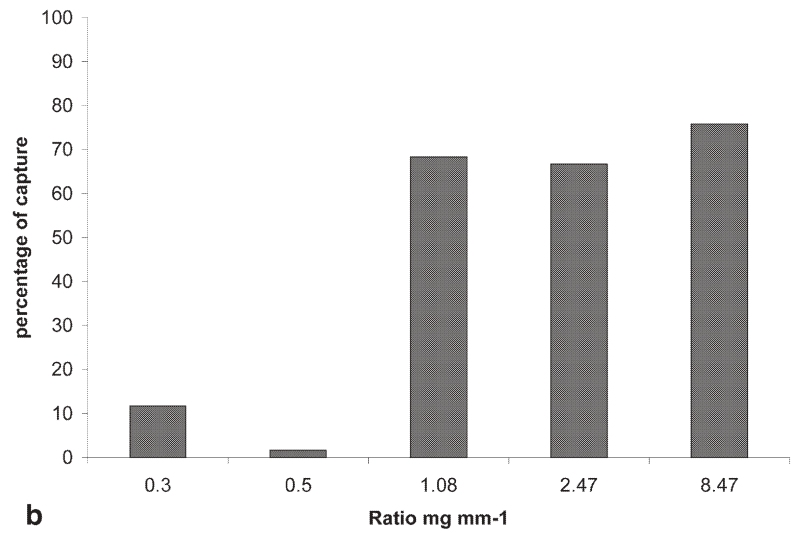
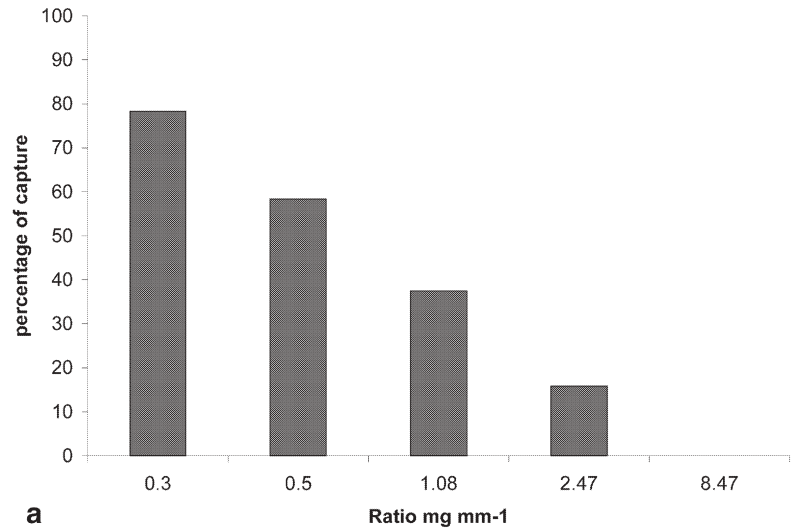
Argyrodes strategies on the *Nephila* web

Argyrodes caudatus frequently attempted gleaning (94% of observations) and was often successful (68% of attempts resulted in prey acquisition). Stealing food bundles or caught prey was rare (1–5% of observations), and feeding with the host was never observed. In *Argyrodes globosus*, gleaning small insects (70% of attempts, 68% of which were successful) and stealing food bundles (21% of attempts, 28% success) were the principal activities, and eating with the host (9% of attempts, 13% success) was also observed. Attempts at stealing caught prey were never observed in *Argyrodes globosus*. The mean time taken to reach *Ceratitis capitata* when scavenging was very similar for both species (mean 22–23 min), whereas prey retrieval was rapid (~ 1 min).

Discussion

The dispersal of *N. clavipes* and associated *Argyrodes* spp. to the coffee plantation caused the *Argyrodes glo-*

Fig. 1 The relationship between the percentage of prey captured by **a** *Leucauge venusta* ($N=120$), and **b** *Nephila clavipes* in respect to the body weight/length ratio (mg mm^{-1}) of the prey caught. **c** Number of prey caught by *Argyrodes* on the web of *N. clavipes* in relation to the body weight/length ratio of the prey.



bosus population already present in coffee to change hosts (Hénaut 2000) in favour of *N. clavipes*. The attractiveness of the webs of *N. clavipes* appears to be due to a combination of three factors. First, small prey are more effectively retained on the web of *N. clavipes* than on the web of *L. venusta*, although *N. clavipes* does not consume them. Thus, the webs of *N. clavipes* were abundant sources of small prey items and large enveloped prey were common. In contrast, the webs of *L. venusta* did not present such foraging opportunities for *Argyrodes* spp. Second, *L. venusta* responds very quickly to prey impact, whereas the comparatively slow-acting *N. clavipes* may offer a temporal window of opportunity for *Argyrodes* foraging at very low risk. Third, the ability of *L. venusta* to detect and respond to small items also means that it acts aggressively to *Argyrodes* spp. (Hénaut 2000) whereas, during the course of our study, we never observed *N. clavipes* acting aggressively towards *Argyrodes* spp.

Host selection in direct response to food availability was reported previously in the association of *Argyrodes* and *Eriophora* sp. (Edgar 1993), but to our knowledge, no previous observations on host selection based on non-aggressive hosts, or slow host response times to prey, have been published. *Argyrodes globosus* often scavenged but also used other strategies to collect food. This range of behaviours was not observed in *Argyrodes globosus* associated with other host species (Hénaut 2000). In contrast, *Argyrodes caudatus* showed a more limited range of strategies, essentially limited to scavenging on the host web.

What prevents all *Argyrodes* species from limiting their behaviour to gleaning insects; probably the lowest risk option available? It may be that gleaning represents a relatively safe strategy but offers a low rate of energetic returns on webs with sparse prey, and requires a large investment in time. As *Nephila* is slow to capture prey and shows little aggression to *Argyrodes* spp., high-return activities are possible, including theft of food bundles containing large prey and even occasional feeding with the host.

The diet of certain species of *Argyrodes* overlaps completely with that of the host and such species should be considered truly kleptoparasitic (Grostal and Walter 1997). However, in our study, there was a clear partitioning of prey between *Argyrodes globosus* and *N. clavipes* based on size/weight ratio. The cost to the host of those *Argyrodes* spp. that do not directly compete for desirable prey items may be neutral, and the relationship may be considered commensal or even mutualistic, as they keep the web clean of unprocessed prey items (Vollrath 1984).

Species-dependent differences in predation and feeding behaviour by the host determine the range of strategies for food acquisition that *Argyrodes* can adopt. Host-dependent variation in prey acquisition strategies was particularly evident in *Argyrodes trigonum* (Cangialosi 1997), and varied from predation of the host and hijacking of the host web, to a kleptoparasitic role, and even the use of its own web for prey capture, depending on the

host species. Moreover, sex and age differences in food acquisition behaviour occur in *Argyrodes ululans*, in which adult females are kleptoparasites of social spiders, whereas the activity of adult males and juveniles is mainly limited to scavenging (Cangialosi 1990).

In association with hosts other than *Nephila*, *Argyrodes globosus* can only act as a kleptoparasite because the host web does not contain unexploited prey items for scavenging. However, *Argyrodes globosus* can modify food acquisition strategies according to the host. Given a choice, *Argyrodes globosus* associates with *Nephila* spp. that permit a low-risk feeding strategy, based on prey selection that does not overlap with that of the host. We conclude that when a kleptobiotic organism has a choice of various host species, it will opt for the least risky host that presents the highest rate of availability of food items. This may explain the marked predisposition of *Argyrodes* to associate with hosts of the genus *Nephila* over the entire geographical range of this genus.

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