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Silk feeding as an alternative foraging tactic in a kleptoparasitic spider under seasonally changing environments

Tadashi Miyashita*, Yasunori Maezono and Aya Shimazaki

Laboratory of Biodiversity Science, School of Agriculture and Life Sciences, University of Tokyo, Tokyo, 113-8656, Japan

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Abstract

Spiders of the genus *Argyrodes* are kleptoparasites that steal prey from other web spiders. Recent studies have shown that in addition to stealing prey, they occasionally eat the silk of the host spider webs. How *Argyrodes* alters the two foraging tactics in the field is still unknown. The foraging behaviour of *Argyrodes flavescens* was observed in the south-western part of Japan where prey availability changes greatly with season. Silk-eating behaviour was commonly observed when insect prey availability on host webs was low, but when prey was abundant, only prey-stealing behaviour was observed. Spiders spent more time feeding on silk than on prey when prey was scarce. Moreover, in the season when most individuals fed on silk, only a small portion of individuals consumed prey. These results suggest that silk eating is an important alternative foraging tactic under seasonally changing environments.

Key words: parasite, host, spider, prey availability, *Argyrodes*

INTRODUCTION

Many animals have alternative foraging strategies whereby they change their foraging methods according to the situations they encounter. Kleptoparasitic behaviours are important foraging strategies for some birds and mammals, but they are usually one of several alternatives, except for bird brood parasitism (e.g. Brockman & Barnard, 1979; Barnard, 1984; Packer & Ruttan, 1988). Some insects and spiders, however, rely entirely on a kleptoparasitic lifestyle (e.g. Vollrath, 1984; Mound, Crespi & Tucker, 1998; Spofford, Kurczewski & Downes, 1989). Some of the well-studied organisms are spiders of the genus *Argyrodes* that live on the webs of 'host' spiders. The unique characteristic of *Argyrodes* is that it uses several different kinds of kleptoparasitic behaviours. They: (1) remove small prey not attacked by the host spider (e.g. Vollrath, 1979; Whitehouse, 1986; Koh & Li, 2002); (2) feed on large prey with the host (e.g. Vollrath, 1979; Whitehouse, 1997; Koh & Li, 2003); (3) remove or usurp prey attacked by the host (e.g. Vollrath, 1979; Cangialosi, 1990); (4) eat the silk of the host spider's web (e.g. Vollrath, 1987; Shinkai, 1988; Koh & Li, 2002). Among them, silk eating seems to be the most impressive because the web provides prey and a place to live for the kleptoparasite as well as being a source of food; web materials contain proteins and other physiologically important compounds (e.g. Tillinghast & Townley, 1987). It would be interesting to know in which situation such a unique behaviour is adopted and how it contributes to the fitness of kleptoparasites. Because consuming silk reduces the area for prey capture and hence would decrease the potential prey that can be stolen, it was expected that silk feeding would be used when prey was scarce.

Recently, silk eating has been found to be common in some *Argyrodes* spiders. Higgins & Buskirk (1998) showed in a laboratory experiment that the amount of web eaten by *A. elevatus* is nearly equivalent to that of prey consumed. Tso & Severinghaus (1998) demonstrated that, although *Argyrodes* consumes 20% of the web area of the host, they do not seem to affect the host's fitness. No studies have ever shown, however, how *Argyrodes* uses the two foraging tactics, i.e. prey stealing and silk feeding, in the field.

Argyrodes flavescens is a kleptoparasite commonly found on various orb-webs and is observed throughout the year in Okinawa, Japan. Because prey availability on host webs changes greatly with season (Miyashita, 2002), this may provide an opportunity to clarify the adaptive significance of this unique behaviour. The questions addressed here are: (1) Is silk eating found more frequently in a season with low prey availability? (2) To what extent does silk eating contribute to the total feeding time of *Argyrodes*?

*All correspondence to: T. Miyashita.
E-mail: tmiya@es.a.u-tokyo.ac.jp

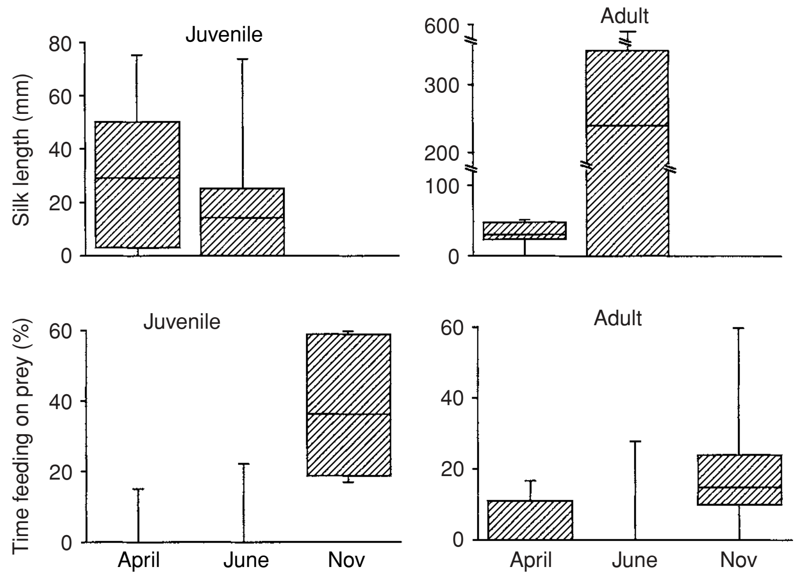

Fig. 1. Seasonal changes in the length of silk eaten/h and the percentage of time spent feeding on insect prey by *Argyrodes flavescens*. Boxes, sample ranges; bars, interquartile ranges.

METHODS

Spiders and study site

Argyrodes flavescens is an orange spider with an adult body length of 2.5–4 mm commonly found on orb webs in Okinawa Island, Japan. Although it occurs throughout the year, the population increases from summer to autumn, probably because the preferable hosts, sub-adult and adult *Nephila maculata* and *N. clavata*, are abundant in this season (Miyashita, 2002). During winter and spring, several spider species can be the hosts for the *Argyrodes*, including *Leucauge blanda*, *Gasteracantha mammosa*, and *Cyclosa confusa* (Miyashita, 2002).

Field observations were conducted at the forest edge in the northern part of Okinawa Island. The climate is sub-tropical, with an average temperature of 22.6 °C and an annual rainfall of 2100 mm. Field surveys were conducted in early April, early June, and early November. Previous observations revealed that small insects left on host webs were very abundant in November, while they were scarce in other seasons (Miyashita, 2002). Because these insects were the main prey for *Argyrodes*, November is the period of abundant food. In early April, the 2 major hosts were absent, but in early June *Nephila maculata* becomes available as a host for *Argyrodes*. Accordingly, although prey on host webs are scarce in June, preferred hosts are available.

Field observations

Behaviours of *A. flavescens* were observed for 2460 min (21 individuals: 11 on *Gasteracantha* and 10 on *Leucauge* webs) in April 1999, 1800 min (12 individuals on *N. maculata* webs) in June 1999, and 2020 min (17 individuals on *N. clavata* webs) in November 1998. Each individual was observed for 90–210 min continuously between 07:00 and 19:00. Observation periods were arranged so that they were distributed evenly between 07:00 and 19:00. The host web observed had no more than 4 *Argyrodes*, so we were able to identify them individually by their body size. Records were made of host body length, vertical and horizontal diameters of the host web, body length of *Argyrodes*, number and body size of prey stolen, feeding duration on prey, length of silk eaten and the number of prey left on the host web. Silk length eaten by *Argyrodes* was measured by tracking the lost part of the thread after each feeding bout. In April, the duration of silk feeding was also measured for 21 individuals.

RESULTS

Time budget

The length of silk eaten/h changed significantly with season (Fig. 1; juvenile: Kruskal–Wallis test, $H = 10.4$, d.f. $= 2$, $P < 0.006$; adult: $H = 13.8$, d.f. $= 2$, $P < 0.001$). In April, 17 of 21 individuals (81%) showed silk feeding, and in June, eight of 12 individuals (67%) fed on silk, while none of the 17 individuals observed fed on silk in November. In particular, silk-feeding activity of adults was extremely high in June, i.e. on average, spiders ate > 300 mm length of silk/h. In April, the lengths of radial and spiral silk eaten were recorded separately for some individuals ($n = 13$), but no significant difference was found (Mann–Whitney test, $U = 104.5$, $P = 0.30$, mean lengths for radial and spiral silk, respectively: 40.5 cm and 21.9 cm).

In contrast to the patterns of web feeding, only a few individuals fed on prey both in April (14%) and

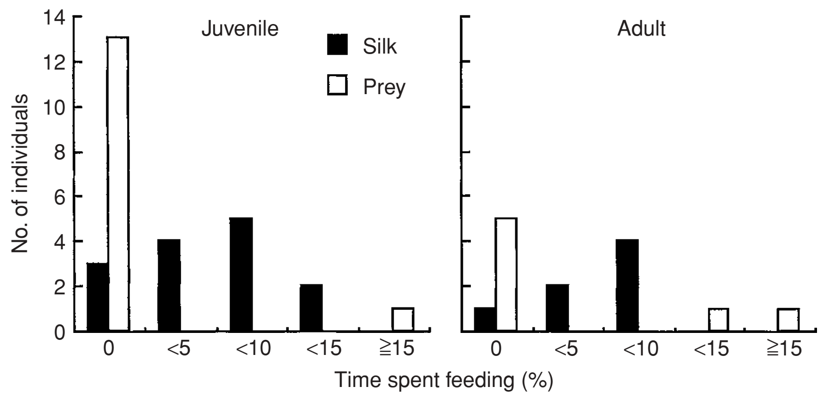

Fig. 2. Frequency distribution in the proportion of time spent on silk feeding *vs* prey feeding by juvenile and adult *Argyrodes flavescens*.

in June (17%). In November, however, most individuals (94%) observed fed on insect prey. Time spent feeding on insect prey changed significantly with the season both for juveniles (Kruskal–Wallis test, $H = 19.6$, d.f. $= 2$, $P < 0.001$) and for adults ($H = 8.9$, d.f. $= 2$, $P < 0.012$).

In April, the time spent feeding on silk as well as on prey was recorded, so the proportions of their feeding time to the total observation time were compared (Fig. 2). Juvenile spiders spent more time feeding on silk than on prey ($U = 33.5$, d.f. $= 1$, $P < 0.001$), while adults showed no difference ($U = 16.5$, d.f. $= 1$, $P = 0.287$), which probably reflects the smaller sample size. When data on juvenile and adult were combined, the difference was still significant ($U = 98$, d.f. $= 1$, $P < 0.001$). The duration of prey feeding, once it was observed, was generally longer than that of feeding on silk.

Prey availability

Differences over time in primary food source (web or insect prey) may be the result of differences in prey availability: the density of prey left on host webs changed seasonally (Kruskal–Wallis test, $H = 20.3$, d.f. $= 2$, $P < 0.001$), with a prominent peak in November (Fig. 3). Most prey were planthoppers, winged aphids, and Nematocera, whose body length was ≤ 2 mm. No instances in which *Argyrodes* stole prey caught by host spiders was observed.

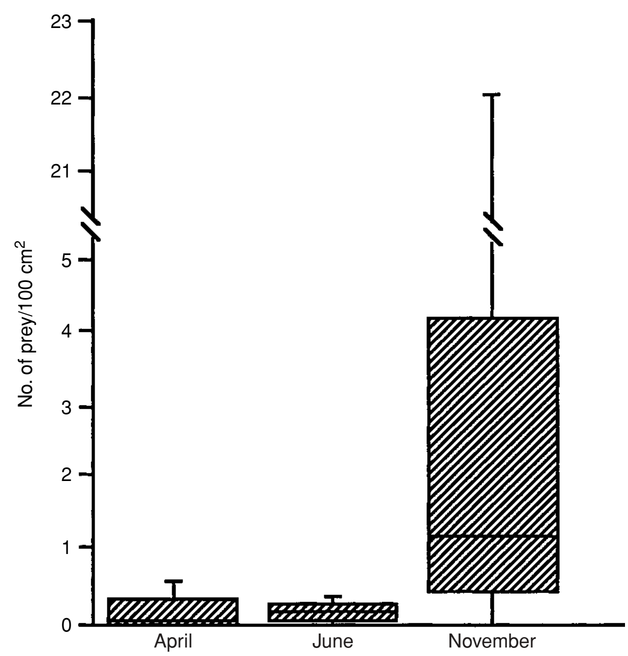

Fig. 3. Seasonal change in the density of prey left on host spider webs. Boxes, sample ranges; bars, interquartile ranges.

DISCUSSION

Argyrodes flavescens fed on insect prey stolen from host web in periods of high prey availability, but often fed on web material when prey was scarce. As far as is known, there has been no report showing such a drastic change in the use of different kleptoparasitic behaviours. One reason for using only prey-stealing behaviour when prey was abundant may be because feeding on insect prey is more efficient than feeding on web materials. This inference was supported by the fact that, once prey feeding was observed, the duration of prey feeding was longer than that of silk feeding, suggesting an advantage of the prey-stealing tactic when prey is abundant. Aside from prey availability, the species of host spider used by *Argyrodes* changed during the season, which might have affected the change in foraging method of *Argyrodes*. Although this possibility is not ruled out, a strong correspondence between the drastic change in prey availability on host webs and the clear shift in foraging method suggests a causal relationship between them.

Higgins & Buskirk (1998) have carried out the only study showing the significance of web eating in *Argyrodes* spiders. They showed that the amount of web material consumed by *A. elevatus* on *Nephila clavipes* webs was nearly equivalent to that of prey consumed by using radio-active-labelled webs and prey. This estimation was, however, performed in controlled laboratory conditions in which both the number of prey and the number of *Argyrodes* were fixed and the host spider had been removed. As mentioned above, the present study revealed that silk eating showed almost no importance when prey was abundant, but the duration of silk feeding was longer than that of prey feeding in April when prey was scarce. Because the amount of silk consumption by adults in June was much larger than that in April while the prey consumptions in June and April were similar, the duration of silk feeding was probably longer than that of prey feeding in June as well. There are no data for the rates of energetic intake per unit time of feeding on silk and prey, so it is premature to conclude that the longer duration of silk feeding reflects a higher energy gain from silk than from prey. It should also be borne in mind that the chemical composition of silk will be different from that of insects. Qualitative differences need to be considered in future studies.

The significance of silk eating should be evaluated not only in terms of the average amount but also its variance. When prey was scarce, most individuals ate silk whereas only a small proportion of individuals consumed prey. This indicates that, although prey stealing seems to bring a great benefit when successful, web eating provides energy constantly at the time of prey shortage, which may reduce the risk of starvation. Because the period of high prey availability is restricted to autumn in Okinawa (Miyashita, 2002), web eating seems to be significant for most of the life cycle of *A. flavescens*.

Another important aspect of silk eating for *Argyrodes* may be that competitively inferior individuals have a chance to get energy from web material. It is known that > 12 individuals can be found on a host web (Elgar, 1988; Miyashita, 2001), and intraspecific competition is severe in *A. flavescens*, forcing smaller individuals to stay at sites where it is difficult to steal prey (Miyashita, 2001). Although no evidence is available, it seems probable that silk eating is an alternative foraging strategy for competitively inferior individuals.

Adult *Argyrodes* exhibited a larger amount of web intake in June than in April, which cannot be explained by prey availability because the number of prey left on host webs was similar between the two seasons. The different silk intake rates may be related to the species of host spider. All the host spiders in June were *Nephila maculata* while those in April were *Gasteracantha mammosa* and *Leucauge blanda*. As the number of both spiral and radial threads was much larger in *Nephila*, the benefit of silk eating might be greater on *Nephila* webs. Another possibility is that the host spiders respond differently to *Argyrodes*. *Leucauge* often responded aggressively toward *Argyrodes* individuals when they were eating the web, whereas such behaviour was seldom observed for *Nephila*. Thus, the interaction between host and kleptoparasite may partly determine which alternative foraging tactics the kleptoparasite uses.

This study demonstrates that silk eating may be an important alternative tactic to prey stealing. As *A. flavescens* uses large orb-web spiders as its hosts, it rarely usurps prey forcefully and eats host spiders. Accordingly, silk eating and prey theft seem to be the main ways of obtaining food. Although both adult and juvenile spiders are seen throughout the year, the prey-rich period is restricted (Miyashita, 2001), and therefore the life cycle might not be possible without web eating. To explore the ecological conditions promoting silk-eating behaviour, the significance of silk eating in different species and in different populations needs to be studied.

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