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OBSERVATIONS ON THE BEHAVIOR OF THE KLEPTOPARASITIC SPIDER, *MYSMENOPSIS FURTIVA* (ARANEAE, MYSMENIDAE)

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Abstract. *Mysmenopsis furtiva,* a tiny spider which lives in the funnelwebs of the Jamaican diplurid spider, *Ischnothele xera,* behaves both as a kleptoparasite and as a commensal; it pilfers portions of its host's prey and also captures and consumes minute insects which are trapped in the host web and unnoticed or ignored by the host. *Mysmenopsis furtiva* is able to ingest hemolymph from its host's prey at a much faster rate than it can ingest material from the insects it captures. Two of its stealth strategies are to move not at all or slowly when the host is motionless and to synchronize its rapid movements with host movements. The host's anti-kleptoparasite behaviors suggest that the kleptoparasite has a significant negative impact on the host.

Kleptoparasitic spiders (those which regularly steal food from other species of spiders) are known to occur in five families (Vollrath 1987; Griswold & Meikle-Griswold 1987): 1) Theridiidae (*Argyrodes* species), 2) Dictynidae (*Archaeodictyna ulova* Griswold and Griswold), 3) Salticidae (*Portia* and *Simaetha* species), 4) Symphytognathidae (*Curimagua bayano* Forster and Platnick), and 5) Mysmenidae. Three genera of mysmenids contain species that are definitely or very probably kleptoparasitic. Two of these, *Isela* and *Kilifia,* are recently described monotypic genera living in the funnelwebs of African diplurid spiders; *Isela okuncana* Griswold is a common kleptoparasite of *Allothele terretis* Tucker (Griswold 1985), and *Kilifia inquilina* Baert and Murphy is a common inhabitant of *Thelechoris karschi* Bösenberg and Lenz webs (Baert & Murphy 1987). In the tropical American genus *Mysmenopsis* (the sister group of *Isela*) three species (*M. ischnamigo* Platnick and Shadab, *M. gamboa* Platnick and Shadab, and *M. dipluramigo* Platnick and Shadab) regularly feed on the prey of their diplurid spider hosts (Vollrath 1987), one (*M. archeri* Platnick and Shadab) feeds on the prey of its pholcid hosts (Baptista 1988), two (*M. capae* Baert and *M. cienga* Müller) have been observed living in *Cyrtophora* webs (Baert 1990), and seven others (*M. palpalis* (Kraus), *M. cidrelicola* (Simon), *M. monticola* Coyle and Meigs, *M. furtiva* Coyle and Meigs, *M. hauscar* Baert, *M. pachacutec* Baert, and *M. tibialis* (Bryant)) have been observed living in diplurid webs (Platnick & Shadab 1978; Coyle & Meigs 1989; Baert 1990; and Alayon pers. comm.). These observations and the evidence for host-kleptoparasite cospeciation in the Jamaican species, *M. monticola* and *M. furtiva* (Coyle & Meigs 1989), suggest that many of the 26 known *Mysmenopsis* species may be found to be obligate kleptoparasites or at least highly dependent on a kleptoparasitic life style.

Although Coyle and Meigs (1989) assumed that the sister species *M. monticola* and *M. furtiva* are kleptoparasites, no direct evidence of kleptoparasitism was available. In this paper we describe observations on the interaction of *M. furtiva* with its host, *Ischnothele xera* Coyle and Meigs, observations which demonstrate conclusively that *M. furtiva* is a kleptoparasite.

METHODS

One adult female *M. furtiva* (body length approximately 1.5 mm) was collected from an *I. xera* web on 20 May 1990 about 15 miles east of Kingston, Jamaica, very near the type locality for both species (Coyle & Meigs 1989, 1990). The kleptoparasite was then transported to our lab in Cullowhee, North Carolina, and released on 25 May into the web of a 14 mm long adult female *I. xera* collected at the same place and time. The host's web was constructed between two vertical panes of glass (15 × 24 cm) separated by 1.5 cm thick strips of wood along the sides and bottoms of the panes. The kleptoparasite and host were observed periodically during daylight hours over the next five weeks, and 9.5 h of behavior were recorded with a Panasonic WV-D5000 video recorder with a Micro-Nikkor 55 mm close-up lens. Live prey, dropped into the host web to trigger prey capture and feeding bouts ($N = 8$), included four mealworm beetle larvae (*Tenebrio,* 11–15 mm long), an adult house cricket (*Acheta domestica,* 16 mm long), three fruit flies (*Drosophila,* 2 mm long), and several booklice and collembolans (1–3 mm long). Estimates of the increase in kleptoparasite abdominal volume during feeding were obtained by measuring the width and length of the abdomen on the video screen before and after feeding, converting these to real dimensions using carapace width as the reference scale, and then computing the abdominal volumes using the equation for an ellipsoid (prolate spheroid), which is similar to the shape of the abdomen. Increase in abdominal volume was then divided by feeding duration to obtain an estimate of the rate of food intake.

RESULTS

The kleptoparasite spent much of the time motionless in a small region of the host's web in the upper half of the arena well away from (10–15 cm) the host's normal resting position in the bottom of the arena. The kleptoparasite did not construct any obvious web, but it should be noted that we did not use methods appropriate for detecting very delicate silk constructs. When moving about the host's web (chiefly during periods of host foraging/feeding activity) the kleptoparasite periodically attached its dragline.

Feeding.—During all three phases of the host prey captures (approach, capture, and carry; Coyle & Ketner 1990) the kleptoparasite either remained motionless, moved slowly, or retreated a short distance away from the activity. Only after the host had returned with the prey to the vicinity of its retreat and had begun feeding did the kleptoparasite move toward the feeding site. Two of these approaches began 1 min after the host commenced feeding (one mealworm capture and the cricket capture); the rest began 9–25 min after.

During two host feeding bouts (mealworm larva and cricket), the kleptoparasite climbed onto the prey while the host was feeding and moved slowly over the prey surface, touching it occasionally with pedipalps and mouthparts as if searching for digestible substrate (Fig. 1). On both occasions the kleptoparasite boarded the prey far from the host's mouthparts; only once did the kleptoparasite approach close to the host's mouthparts, but it made no attempt to feed there. We observed the kleptoparasite feeding on host prey three times. In the first instance, while the host fed on the neck of the cricket, the kleptoparasite fed on hemolymph seeping from the base of the cricket's third leg, which we had removed before dropping the cricket into the web. During this feeding, which lasted 16.5 min, the volume of the kleptoparasite's abdomen more than doubled, increasing by approximately 0.72 mm^3, for an intake rate of 0.044 ml/min. Three and a half hours later, while the host was feeding on the cricket's body, the kleptoparasite fed very briefly on the neck region of the cricket's head, which had been removed by the host. Several days later during another host feeding bout, the kleptoparasite fed on fluid (presumably hemolymph) at the host-severed end of half a mealworm while the host fed on the other half nearby. This feeding lasted 10.1 min, not including two brief pauses near the end of the feeding bout, and doubled the kleptoparasite's abdominal volume, increasing it by approximately 0.86 mm^3, for an intake rate of 0.085 ml/min. Whenever the kleptoparasite fed, its legs and pedipalps were motionless but its abdomen usually swayed slowly and slightly.

We attempted to determine whether the kleptoparasite would capture small prey on its own. When we dropped three fruit flies onto the host web, the host captured all three within a few minutes and the kleptoparasite remained virtually motionless. At another time we dropped some collembolans and booklice onto the web, the host captured and fed on the largest collembolan, and the kleptoparasite did not approach any of the insects. On another day we dropped a very small booklouse (about half the volume of the kleptoparasite) and two collembolans (a sminthurid and an entomobryid, each about one-third to half the volume of the kleptoparasite) onto the web. The host did not respond, but, after about 7 min, the kleptoparasite began to approach and eventually captured (grabbed with its first legs and bit) and consumed the booklouse. During this 83 min feeding bout, the kleptoparasite's abdomen increased slightly in volume, by approximately 0.19 mm^3 for an intake rate of 0.002 ml/min. It then proceeded in a similar manner to capture and consume the two collembolans, feeding on the first for 80 min. Since these two feeding episodes were not video-recorded, it was

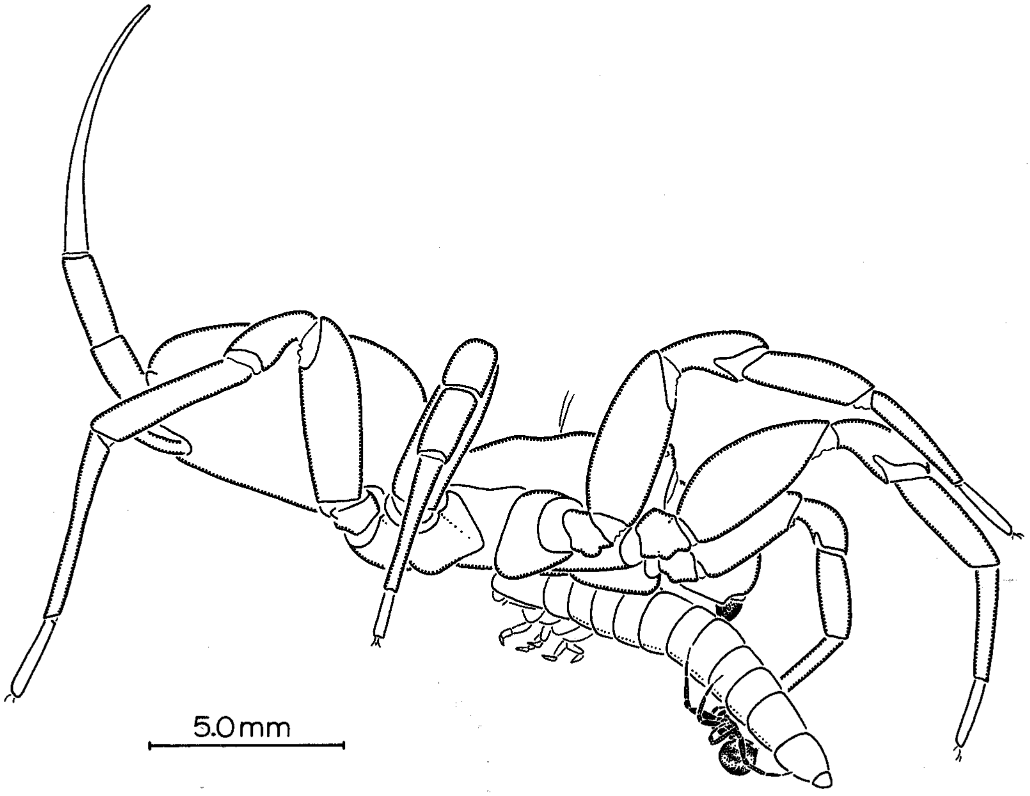

Figure 1.—Adult female *Mysmenopsis furtiva* searching for a feeding site on a *Tenebrio* larva, which is being consumed by an adult female *Ischnothele xera.*

not possible to obtain abdominal volume increase estimates, but the increases appeared small.

Occasionally the kleptoparasite repeatedly reached with its legs and gathered a few fine strands of silk to its mouthparts. Whether the spider was simply breaking strands to reduce a small region of the host web or actually digesting *and* ingesting web protein could not be determined.

Kleptoparasite movements.—The form and speed of kleptoparasite movement through the web depended markedly on the host's behavior. When the host was not moving, kleptoparasite movements were typically slow, especially if the host was not feeding. During such slow movement, rarely did more than two or three legs move at a time, and forward progress, when it occurred, was only 0.2–0.6 body lengths per second (mean = 0.41 ± 0.12, $N = 11$). Slow movements typically involved rather slow waving and probing motions of the legs, particularly the anterior pairs. Rapid kleptoparasite movements occurred only when the host was moving (ambulatory and prey manipulation movements) and consisted of very short advances and/or rapid leg waving/probing as well as (less commonly) longer advances. Forward progress was much faster during these advances than during slow advances, ranging from 3.0–11.1 body lengths per second (mean = 5.44 ± 2.57, $N = 7$).

During one bout of host feeding when both kleptoparasite and host behaviors were simultaneously recorded, we tallied whether or not kleptoparasite movements occurred during host movements; every one of the 116 rapid (and many of the slow) kleptoparasite movement events occurred during host movement. The onset and cessation of most of these kleptoparasite movements coincided with the beginning and end of the host movements. On occasion, when the host was feeding, the kleptoparasite would make moderately fast movements (1.0–1.7 body lengths per second, $N = 3$) while the host was not moving, but this usually (over 75% of the time) happened when there was a large prey item or dense silk between the kleptoparasite and the host.

Host responses to the kleptoparasite.—While the host was feeding, we observed certain host behaviors that do not normally occur during feeding in a kleptoparasite-free web, and were therefore almost certainly anti-kleptoparasite behaviors. *Silk application:* On 20 occasions the host interrupted feeding and applied silk to its web, usually in the region between the kleptoparasite and its feeding site (and/or unattended pieces of prey). Frequently, much silk was applied (spinning duration = 7–113 s, mean = 25 ± 28.1, $N = 12$). *Scouting/challenging:* On 13 occasions the host released its prey, dashed or walked quickly partway toward the kleptoparasite (which was usually approaching the host's feeding site or an unattended portion of prey), paused, and then returned to the feeding site. The non-persistent nature of this approach seems to distinguish it from a prey capture approach. Sometimes the kleptoparasite retreated in response to the host's advance. Occasionally the host paused to apply silk during her return. *Agitated feeding:* When the kleptoparasite was moving very close to or on the prey while the host was feeding, prey manipulation by the host usually increased in frequency and intensity and was sometimes accompanied by brief rapid tapping of pedipalps on the prey or at the kleptoparasite. Sometimes the kleptoparasite retreated during these host behaviors. On a few occasions the host suddenly carried the prey to a new position, leaving the kleptoparasite behind. *Web-biting:* On five occasions the host turned toward the kleptoparasite, pulled part of the web toward its chelicerae with its pedipalps, and quickly extended and flexed its fangs into the silk in a biting movement. *Chasing:* Three times we observed the host chasing after the kleptoparasite, but every chase was short and quickly aborted. The riskiest such challenge for the kleptoparasite involved the host lunging and striking at the spot where the kleptoparasite had started its narrow escape, and then feeding on the piece of prey on which the kleptoparasite had been feeding.

DISCUSSION

Our observations show clearly that *M. furtiva* is a kleptoparasite which readily approaches and feeds upon prey captured by its host. Its feeding does not require assistance from host digestive enzymes, as evidenced by the kleptoparasite's successful ingestion of hemolymph at the cricket's leg base, which had not been fed upon by the host, and by its capture and consumption of minute insects. Its stealthy behavior is also indicative of a spider specialized for kleptoparasitism. Particularly noteworthy is its practice of moving quickly only when the host is moving, a stealth strategy also employed by *Argyrodes elevatus* Taczanowski (Vollrath 1979) and one which presumably takes advantage of the host's probable inability to separate informative web vibrations from those it is generating. The possibility that we observed *M. furtiva* ingesting its host's silk needs to be further explored; at least three *Argyrodes* species feed on host silk (Vollrath 1981, 1987; Whitehouse 1986).

Our observations reveal that *M. furtiva* is also an opportunistic predator which can detect, capture, and ingest tiny insects which are caught in the host's web and are unnoticed or ignored by the host. The same capability has been observed in kleptoparasitic *Mysmenopsis* species (*M. ischnamigo, M. gamboa,* and *M. dipluramigo*) living in diplurid webs in Panama (Vollrath 1978, 1987). It would be interesting to know whether this kind of commensalistic activity is a common and/or crucial source of nutrition.

Clearly, this kleptoparasite ingested much more material per unit of feeding time from host prey than from the tiny insects it captured. The apparent costs to *M. furtiva* of feeding as a kleptoparasite (especially the risk of being captured by the host) may be at least partly compensated by the advantages of feeding on hemolymph, i.e., rapid ingestion and low digestive costs. Not only can hemolymph be ingested without the time, energy, and material costs of external digestion, but many of its constituents are small molecules which can be digested inexpensively. A cost/benefit analysis of these alternate feeding strategies should also consider the nutritional value of the ingested food; since insect hemolymph is very similar to intracellular fluids and contains relatively high concentrations of amino acids, organic phosphates, proteins, and carbohydrates (Florkin & Jeuniaux 1974; Mullins 1985), it may be nearly as valuable nutritionally per volume as muscle and other tissues that are digested during the consumption of minute prey.

Our observations suggest that *Mysmenopsis* kleptoparasites, in spite of their small size, may have an important negative impact upon their hosts. Food stealing, the interruption of host feeding, and the host's (partly effective) anti-kleptoparasite efforts, some of which are also performed by the diplurid hosts of other *Mysmenopsis* species (Vollrath 1978, 1979, 1984), must increase the cost/benefit ratio of feeding for the host. Just the existence of such anti-kleptoparasite behaviors is indicative of a negative effect by the kleptoparasite. When several *Mysmenopsis* adults and juveniles live together in one web (a common situation in webs of the diplurids Vollrath (1984) observed, adult female *Ischnothele reggae* Coyle and Meigs (Coyle & Meigs 1989), and probably also *I. xera*), the collective cost to the host could be particularly important.

We suspect that a key reason why diplurid webs are especially favorable for mysmenid kleptoparasites is their persistence in time and space. The first author's field observations indicate that adult female diplurids commonly occupy the same web for one or more years. In addition, the fine dense mesh, large size, asymmetry, and three-dimensional nature of these webs, as well as the high ratio of host size/kleptoparasite size (Fig. 1), should make it easier for a kleptoparasite to avoid detection and capture.

These observations trigger many questions. How important is the capture of tiny prey to the economy of the kleptoparasite? Exactly how does a group of these kleptoparasites affect the host? Do the kleptoparasites interact aggressively, tolerate one another, or cooperate? How effective are the host's anti-kleptoparasite tactics? What regulates the number of kleptoparasites in a web? Further study of the interactions among these mysmenid kleptoparasites and their hosts should provide useful insights into the behavioral ecology of kleptoparasitism and host-symbiont coevolution.

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