

SHORT COMMUNICATION

Stealing for love? Apparent nuptial gift behavior in a kleptoparasitic spider

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Abstract. The presentation of nutritional resources as nuptial gifts before or during the mating process is well known among insects, but has only rarely been documented in spiders. Here, we report on observations and a series of photographs made during field studies in Fortin de las Flores, Veracruz, Mexico, which, although a single anecdotal report, represent a potentially significant finding. A male of the kleptoparasitic spider *Argyrodes elevatus* Taczanowski 1873 (Araneae, Theridiidae) was observed stealing a prey item from within a communal web of its host, the colonial orb-weaver *Metepeira incrassata* F.O. Pickard-Cambridge 1903 (Araneae, Araneidae). The male *A. elevatus* then carried and presented the prey item to a female, waited nearby until she began feeding, and copulated with her as she fed upon it. As far as is known, this is the first report of kleptoparasitic *Argyrodes* apparently utilizing a prey item stolen from a host spider as a nuptial gift.

Keywords: *Argyrodes*, nuptial feeding, colonial spiders, *Metepeira*

In many arthropod species, the courtship and mating process includes some form of provision of nutritional resources, either as nuptial feeding or nuptial gifts offered before, during or immediately following copulation (Boggs 1990; Vahed 1998; Gwynne 2008). Presentation of nuptial gifts has only rarely been documented in spiders, and is limited to two families, the Pisauridae and Trechaleidae. Nuptial gifts are best known for *Pisaura mirabilis* (Clerck 1757) (Stålhandske 2001, 2002), but similar nuptial offerings during courtship have been reported for two additional pisaurids, *Pisaurina lama* Bosenberg and Strand 1906 (Itakura 1993) and *Perenethis fascigera* (Bosenberg and Strand 1906) (Itakura 1998). Most recently, a study of nuptial gifts in two species of the closely-related family Trechaleidae, *Paratrechalea azul* Carico 2005 and *Paratrechalea ornata* (Mello-Leitao 1943) has revealed a similar provisioning behavior during courtship (Costa-Schmidt et al. 2008).

During our field studies in Mexico, we observed the unusual behavior described below, which represents the first report of kleptoparasitic *Argyrodes* apparently utilizing a prey item stolen from a host spider as a nuptial gift. Spiders of the genus *Argyrodes* are well known as kleptoparasites on other spiders and are frequently found in association with many web-building spider species (see reviews in Higgins & Buskirk 1998; Whitehouse et al. 2002; Agnarsson 2002). A number of species of *Argyrodes* are associated with colonial and social spiders and may represent a cost of group-living from prey loss and predation (Elgar 1989; Cangialosi 1991; Whitehouse & Lubin 2005). This is certainly true for the colonial orb-weaver *Metepeira incrassata* F.O. Pickard-Cambridge 1903, which serves as host to six species of Argyrodinae (McCrate & Uetz 2009).

The observations reported here were made at a coffee plantation near Fortin de las Flores, Veracruz, Mexico (18°53'54.30"N, 96°59'30.92"W), used in several previous studies of colonial *M. incrassata* (see Uetz & Hodge 1990; Rayor & Uetz 1990, 1993, 2000; Uetz et al. 1994; Uetz & Hieber 1994; Jakob et al. 2001; Uetz et al. 2002; Hieber et al. 2002). Observations were made during mid-day on 13 July 1991, in a colony of approximately 300 *M. incrassata*, as part of a study of *Argyrodes* kleptoparasitism (A. McCrate, M.S. Thesis 1996). Photographs of the behaviors described below were taken using a Nikon FM 35mm SLR film camera and represent a sequence of 23 slides, taken over a period of several minutes. The specimens were captured and preserved, and later identified by Scott Larcher and Dawn Southard at the Smithsonian National Museum of Natural History as *Argyrodes elevatus* Taczanowski 1873.

A male *A. elevatus* was observed stealing a recently captured and wrapped prey item from a host spider within a communal web of the colonial orb-weaver *M. incrassata*. The male *A. elevatus* carried the prey item (Fig. 1a) in the manner typical for members of this genus, trailing behind the spider on silk attached to the spinnerets (Vollrath 1979a, 1984; Whitehouse 1997). The male moved toward a female *A. elevatus* within the colony that was initially moving in a direction away from the male at a distance of 30–40 cm, following her path along strands of the communal web. The male approached the female to a distance of approximately three body lengths (1–2 cm) and stopped. At this time, the male removed the prey item from its trailing position behind the abdomen with the forelegs and used its mouthparts to position the prey item on the silk line ca 1.0 cm directly in front of the female (Fig. 1b). The female turned around, and the male left the prey item behind (Fig. 1c), then waited nearby (< 1.5 cm). The female approached the prey item, commenced palpating the prey with her mouthparts, and began feeding, after which the male approached (Fig. 1d). The male then assumed a face-to-face mating position (Fig. 1e) and copulated with the female while she fed. Feeding by the female during copulation was intermittent, but intromission continued even when the female released the prey item (Fig. 1f). This behavior is different from pre-contact courtship behavior reported for other *Argyrodes* species (Cangialosi 1990; Whitehouse 1994; Whitehouse & Jackson 1994), and to our knowledge, this apparent nuptial gift behavior is the first report for *A. elevatus* or any other *Argyrodes* or theridiid species.

An alternative explanation (to nuptial gift behavior) might be that this observation represents a means of avoiding aggression, i.e., the smaller male abandoned its prey item in the presence of a larger female. Or, it might also be possible that *A. elevatus* males sometimes engage in mating behavior by approaching and copulating with females while they are feeding. However, both mating and agonistic interactions among *Argyrodes*, described in detail for other species, usually involve complex behaviors not seen here (Cangialosi 1990; Whitehouse 1994; Whitehouse & Jackson 1994). We believe that this unique observation represents nuptial gift exchange in *A. elevatus* for several reasons: 1) the male followed and approached a moving female, as is typical in the first phases of *Argyrodes* courtship (Cangialosi 1990; Whitehouse 1994; Whitehouse & Jackson 1994); 2) the male behaviors observed are clearly different from those seen in other phases of courtship and mating described for *Argyrodes* species, which typically include leg-waving, rotary probing and other



Figure 1.—Selected photographs from a sequence taken in the field illustrating male nuptial gift behavior in *A. elevatus*: a. male dragging stolen prey item (an unidentified hymenopteran); b. male presenting prey item in a position near the female; c. male leaving prey item to wait nearby; d. male approaching female as she accepts, palpates and begins to feed upon the prey item; e. male positioning to insert palp; f. copulation.

behaviors (Cangialosi 1990; Whitehouse 1994; Whitehouse & Jackson 1994), which were not seen in this event; 3) the presentation was obvious and appeared intentional (i.e., the male removed the prey item from the spinnerets, held it with mouthparts and directed it toward the female); and 4) although different from other reports of nuptial gift behavior in spiders (Anderson et al. 2008), acceptance of the gift in this manner by the female was atypical of *Argyrodes* foraging behavior, as she swiftly turned to face the male, grasped the

prey item and began feeding without carrying it away (Vollrath 1979a,b, 1984; Cangialosi 1990, 1991; Whitehouse 1994, 1997). Given that this observation is so distinctly different from the well-documented mating behavior patterns of other *Argyrodes* species, we suggest that the apparent nuptial gift of *A. elevatus* could represent an alternative mating tactic for *A. elevatus*.

The contribution of a nuptial gift may enhance male fitness, and several hypotheses have been offered to explain their adaptive value

for arthropods, including spiders: 1) paternal investment via nutritional contribution to offspring fitness (Thornhill 1976); 2) sexual selection for male mating effort, resulting in increased fertilization success via prolonged copulation (Austad & Thornhill 1986; Stålhandske 2001; Huber 2005); 3) male exploitation of female sensory biases (Stålhandske 2002; Sakaluk et al. 2006; Bilde et al. 2007; Vahed 2007); and 4) protection from sexual cannibalism (Bristowe 1958; Vahed 1998; Stålhandske 2001). Recent experimental evidence for *P. mirabilis* supports the mating effort hypothesis, while refuting the defense against cannibalism and paternal investment in offspring fitness hypotheses (Anderson et al. 2008). The question of whether a nuptial gift of a wrapped prey item represents sensory exploitation by its resemblance to a female's egg sac is doubtful, as female *P. mirabilis* more readily accepted unwrapped prey (Anderson et al. 2008). However, these hypotheses may not be mutually exclusive, as presentation of a prey item as a nuptial gift may exploit sensory aspects of the female's foraging behavior, thereby occupying her attention while the male attempts mating (Stålhandske 2002; Vahed 2007; Bilde et al. 2007; Anderson et al. 2008). While most of these hypotheses apply to our observation, it is not possible to refute any with a single observation such as this. We might speculate that a combination of several of these hypotheses applies here. For example, it is possible that our observation of *A. elevatus* represents some form of sensory exploitation, as this species is kleptoparasitic, and exploits prey wrapped in silk by host spiders and hanging in the web. While a wrapped prey item suspended in the *M. incrassata* colonial web near a female might be a likely target for kleptoparasitism, a male presenting a prey item in this manner might also produce vibratory stimuli that attract female attention, and thereby exploit a pre-existing sensory bias of the female. By presenting a nuptial gift in this manner, male *Argyrodes* might avoid female aggressive attacks or potentially cannibalism (Whitehouse 1994) and subsequently allow copulation while the female feeds. Ultimately, since the female fed upon the prey item while copulating, the apparent nuptial gift would likely contribute material resources to offspring (Bilde et al. 2007).

Given that this is a single observation, any adaptive explanation is speculative and should be interpreted with caution. We observed this behavior only once in thousands of hours of observation of *Metepeira incrassata* (and hundreds of hours by ACM observing *Argyrodes*) in the field, although our primary interest was the other behaviors, and thus it is hard to gauge its true frequency. However, a recent (and independent) observation of similar behavior by *A. elevatus* in a colonial orb-weaver colony in South America (Cobbold & Su, unpubl. manuscript) would appear to corroborate that our observation was not an artifact. Although this anecdotal report of a single observation raises many questions that cannot be answered here, we believe it represents a significant finding worthy of future investigation.

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