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Sex-role reversed nuptial feeding reduces male kleptoparasitism of females in Zeus bugs (Heteroptera; Veliidae)

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Males of a variety of taxa occasionally steal food secured by their mates. In some spiders and insects, males rely entirely on this form of intraspecific kleptoparasitism for their subsistence. However, this male strategy may be costly for females and a variety of different female counteradaptations have been proposed. In Zeus bugs (*Phoreticovelia* spp.), males ride on the back of their mates for extended periods and females produce a gland secretion that males feed on. By experimentally occluding the dorsal glands in females and varying food availability, we show that nuptial feeding by females reduces the extent to which the males kleptoparasitize their mates. We suggest that females have, at least in part, evolved this unique form of nuptial feeding as a counteradaptation to reduce the rate of kleptoparasitism by males.

Keywords: sexual conflict;
sexually antagonistic coevolution; sperm competition;
sexual selection; mating system

1. INTRODUCTION

Reproductive competition among males may select for a variety of traits or strategies that cause direct harm, or are otherwise costly, to their mates (Parker 1979; Morrow *et al.* 2003). Such traits may be sexually antagonistic, in which case, the females are selected to minimize direct costs imposed by males as a result of sexual conflict (Arnqvist & Rowe 2005). One type of male behaviour that may be potentially costly to their mates is kleptoparasitism. The male habit of stealing or sharing prey items or food captured/collected by females is widespread in certain taxa. For example, in some lion (*Panthera leo*) populations, pride males rarely hunt and instead share or steal prey brought down by their pride females (e.g. Funston *et al.* 1998). In many insects, males ride passively on the back of their mates for extended periods as a form of postcopulatory mate guarding (see Alcock 1994) and males of some species may then feed on food/prey secured by the female (e.g. Sattler 1957). Kleptoparasitism by males is particularly common among spiders where males cohabit with females on or near their webs for extended periods, during which males often feed on prey caught in the webs of females (see Schneider & Lubin 1998 for a review). In the eresid spider *Stegodyphus lineatus*, such kleptoparasitism is clearly costly for females: females with cohabiting males weigh less, in part as a result of prey stealing by males (Erez *et al.* 2005). The costs of kleptoparasitism by males to females may be widespread, as a result of the male-imposed reduction in foraging efficiency. Consequently, a variety of putative female counteradaptations have been suggested. These include reducing their attractiveness to males (Watson 1990), aggression/resistance towards kleptoparasitic males (Erez *et al.* 2005) and avoidance of males through relocation (Lubin *et al.* 1993).

In Zeus bugs, *Phoreticovelia* spp. (Heteroptera; Veliidae), a genus of small (1–2 mm) and elusive semiaquatic bugs, sexual size dimorphism is very pronounced (Polhemus & Polhemus 2000; Andersen & Weir 2001). The much smaller males ride on the back of their mates for as much as several weeks (see Arnqvist *et al.* 2003, submitted). Remarkably enough, females, but not males, are equipped with a pair of dorsal glands that produce a wax-like secretion that males feed from when riding on the backs of their mates (Arnqvist *et al.* 2003). However, the adaptive significance of this unique form of sex-role reversed nuptial feeding is puzzling. Females can store sperm for long periods (Arnqvist *et al.* 2003) and natural populations are dense and show a male-biased sex ratio (Arnqvist *et al.* submitted), so it is unlikely that males represent a valuable insurance against a shortage of viable sperm for females. Males in captive populations frequently kleptoparasitize their mates (inserts in figure 1), suggesting that nuptial feeding may instead represent a female counteradaptation, which decreases the rate of kleptoparasitism by males. Here, we provide an experimental test of this hypothesis.

2. MATERIAL AND METHODS

The Zeus bugs used in this experiment were collected in the Little Mulgrave River, Queensland, Australia, and were brought into the laboratory. Prior to the experiments reported here, all the bugs were kept in aerated 30×40 cm tanks (water depth 10 cm) provided with balsa wood floaters (as resting sites) and ample food (frozen cricket nymphs and *Drosophila* fruit flies). All were apterous, adult *Phoreticovelia disparata*.

We studied the independent effects of food availability and nuptial feeding on the rate of kleptoparasitism by males using an orthogonal 2×2 analysis of variance design that altered the feeding regime of females and male access to their glandular secretions ($n=10$ pairs per treatment combination; total $n=40$ pairs). At day 0, the females were isolated individually in cups (water depth 3 cm) provided with a paper strip as a resting site and were randomly assigned to either of the following treatments. We varied the feeding regime, by providing females with either one frozen cricket nymph per day or no food. Half of the females had their dorsal glands occluded by covering the glandular openings, located on the mesonotum, with a thin layer of water-based Enamel model paint. To control the effects of paint, the other half instead had the same amount of paint applied to their tergites. A single male was then introduced to each female.

In the morning at day 2, all prey items were removed from the pairs. During the afternoon, we then performed assays of the kleptoparasitic behaviour of males by adding a fresh frozen cricket nymph into each cup, while observing the behaviour of the bugs under a dissecting microscope. We recorded the duration of the ensuing female feeding session and the duration of male kleptoparasitic feeding during this session. Following these behavioural assays, each pair was kept under their food regime and male survival was checked daily until all males had died in order to determine male lifespan.

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Table 1. The effects of food provisioning and nuptial feeding by females on the extent of kleptoparasitic behaviour of their mates. The residuals of these models were not significantly different from normality (Shapiro–Wilk's test; $p=0.773$ and 0.063, respectively).

	duration of kleptoparasitic feeding by males				proportion of female-feeding session that was kleptoparasitic[a]			
source	SS	d.f.	F	p	SS	d.f.	F	p
feeding regime	53 909	1	13.72	0.002	0.606	1	8.73	0.009
gland occlusion	19 829	1	5.05	0.038	0.615	1	8.85	0.008
feeding regime × gland occlusion	26 560	1	6.76	0.019	0.172	1	2.48	0.134
error	66 791	17			1.181	17		

[a] Arcsine transformed prior to analysis.

3. RESULTS

Kleptoparasitism by males was very common: males riding females invariably 'shared' the prey item of their mates during our behavioural assays. However, the degree of kleptoparasitism increased with both occlusion of the dorsal glands and with previous starvation of the female (table 1; figure 1). This was true irrespective of whether male kleptoparasitism was measured as absolute male-feeding duration or the proportion of the female-feeding session during which the male was feeding on the prey item. Further, the effect of gland occlusion on kleptoparasitism was more pronounced when females had been starved, as indicated by a significant interaction between the two factors on the duration of kleptoparasitism (table 1).

Males with females provided with food lived for longer (5.9 days, s.e. $=0.29$) than did those with starved females (2.85 days, s.e. $=0.29$; $F_{1,36}=53.93$, $p<0.001$). However, neither female gland occlusion ($F_{1,36}=0.13$, $p=0.72$) nor the interaction between these factors ($F_{1,36}=0.01$, $p=0.90$) affected male lifespan significantly.

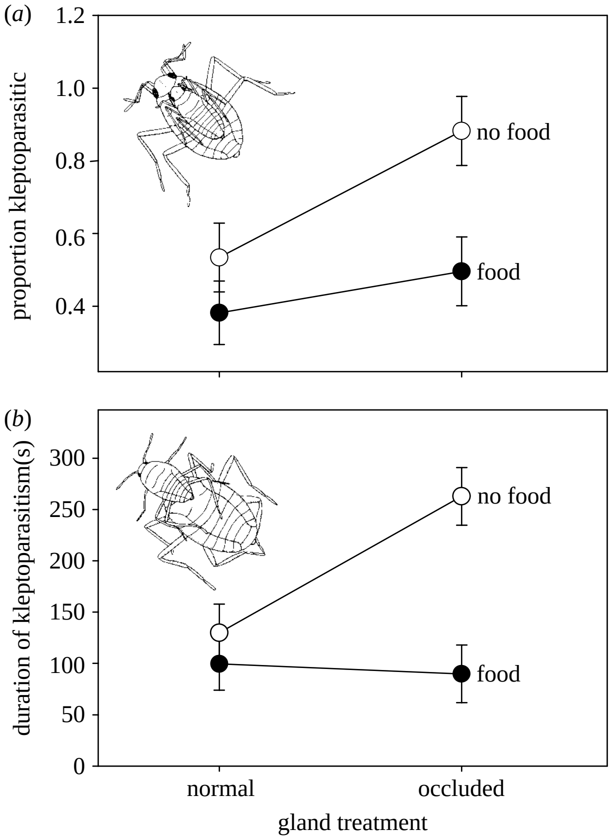

Figure 1. When a Zeus bug female starts feeding on a prey item while resting on the water surface, the male, which normally rests firmly attached on the female abdomen (insert in *a*), crawls to the front of the female, leans over, probes the prey item with his mouth parts and starts feeding (insert in *b*). The figure shows the effects of occlusion of female dorsal glands and prior food provisioning on (*a*) the proportion of female-feeding sessions during which the male also feeds on the prey and (*b*) the absolute duration of male feeding on female prey items. LS means ± s.e.

4. DISCUSSION

In natural Zeus bug populations, male–male competition for single females is intense because adult sex ratios are markedly male biased and virtually all adult females are ridden by males (Arnqvist *et al.* submitted). Presumably, the large number of adult males found riding juvenile females that are still reproductively immature (Arnqvist *et al.* submitted) reflects this level of reproductive competition. Thus, kleptoparasitism benefits a male by allowing him to remain on his mate without being food deprived, thereby reducing his risk of sperm competition (Alcock 1994), despite any potential costs that this may bring to his mate (Parker 1979; Morrow *et al.* 2003). The fact that our food treatment increased the lifespan of males riding females with occluded glands is in line with this conclusion. Although we found no significant effect of female gland occlusion *per se* on male lifespan here, an earlier experiment showed that the lifespan of starved males increased markedly when allowed to ride a female compared with when kept alone (Arnqvist *et al.* 2003).

In an earlier study, using female Zeus bugs which had been fed radiolabelled food, we demonstrated that males feed on the secretions produced by the dorsal glands of females (Arnqvist *et al.* 2003). The current experiments show that when these glands are occluded, the extent to which males kleptoparasitize their mates increases significantly. These results reveal that one of the current effects of these glands is to reduce kleptoparasitism by males, and that the rate of kleptoparasitism increased with decreasing food availability. This effect was more pronounced among females with occluded glands, which indicates that this was not due to starved females producing less nuptial food, but rather a direct effect of male hunger as a result of a previous lack of opportunities to kleptoparasitize females.

Since glandular secretions decrease kleptoparasitism, we suggest that the unique form of nuptial feeding in Zeus bugs may have evolved, at least in part, to reduce the degree of kleptoparasitism by males. Although females of a variety of taxa have a suite of different traits to reduce the direct costs imposed by males, the present study would then represent the first experimental demonstration of an apparent female counteradaptation to kleptoparasitism by males. However, we note that two conditions must be fulfilled for this to be a logical evolutionary interpretation. First, kleptoparasitism by males should be costly to females. Although we have no direct data on the costs of kleptoparasitism to female Zeus bugs, the experimental studies have shown that food is a limiting factor in natural populations of other semiaquatic insects (Spence 1986) and our field observations of Zeus bugs suggest that they prey on very small prey items. Second, in order for nuptial feeding to minimize costs to females, the costs of producing gland secretion should be lower than those of being kleptoparasitized. A chemical analysis of the content of the gland secretion is underway, which will help in assessing these costs. Needless to say, our experiments do not exclude the possibility that the glandular secretions produced by females have additional functions. These include, for example, to reduce direct costs of other types of male harm, to help keep a satiated male rather than having it replaced with a hungry male, to protect against pathogens or predators, or for grooming and/or chemical communication.

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