Reversal of sex roles in nuptial feeding

Female Zeus bugs subvert the traditional notion that amorous gifts are a male preserve.

Males of many animals provide females with 'nuptial gifts', such as prey items or glandular secretions, during courtship and mating[1]. Traditionally, nuptial feeding is viewed as a form of paternal investment in offspring[2–4]. Although other explanations have been proposed[5–7], the focus remains gender-specific, with a male donor and female recipient. Here we show that females of the extraordinary insect *Phoreticovelia disparata* provide food for males during mating. This previously undescribed reversal of gender roles indicates that nuptial feeding might not be related to paternal investment.

The recently discovered genus *Phoreticovelia* (Heteroptera; Veliidae)[8,9] consists of semi-aquatic insects that inhabit tropical rivers. They are gregarious and nocturnal predators; swarms scavenge the water surface at night for food. Female morphology and the mating habits of these Zeus bugs (so called because, according to legend, Zeus consumed his first wife, Metis) indicate that males might be feeding on female glandular secretions during mating (Fig. 1).

We tested this possibility by using *P. disparata* collected from the Upper Mulgrave River, Queensland, Australia. We first primed individual females kept with or without males by feeding them on radiolabelled (^{3}H) or non-labelled *Drosophila melanogaster* for 10 days (n was 16, 17, 19 and 20, respectively). New focal males were then allowed to ride females for four days while they were offered only non-labelled food. All focal individuals were subsequently dissolved (in 100 μl 50 mM NaOH and 5 ml scintillation fluid) and the amount of radioactive label was measured in a scintillation analyser.

Focal males riding females fed with non-labelled food did not contain any label (males versus control vials; t-test, d.f. = 44, $P = 0.819$). However, focal males riding labelled females contained labelled material (mean d.p.m. (adjusted for background radiation) ± standard error; 11.14 ± 1.48 versus −0.58 ± 0.46; ANOVA, $F_{1,68} = 65.03$, $P < 0.001$), irrespective of the presence or absence of a male during priming ($F_{1,68} = 0.51$, $P = 0.474$). This confirms that material passed from the female to the male, at a rate consistent with the male consuming a few per cent of his body weight of female gland secretion per day.

Females produce glandular secretions only when ridden by a male. We removed all glandular secretions from females (Fig. 1a), isolated them individually with or without a male ($n = 10$ for both) for 13 days, and then scored the distribution of glandular secretion. The former, but not the latter, females regenerated their patches (Mann–Whitney U-test; $P = 0.002$). Further, the lifespan of starved males increased by about 50% when they were kept with a female compared with those kept alone (2.4 ± 0.2 versus 1.6 ± 0.2 days; t-test, $P = 0.014$), but there was no significant difference in survival when males were fed (10.6 ± 1.4 versus 13.1 ± 1.6 days; t-test, $P = 0.252$; ANOVA interaction, $F_{1,79} = 3.99$, $P = 0.049$), suggesting that males benefit from feeding on females.

We also monitored the lifetime reproductive performance of individual females (fed with one cricket nymph per day) kept with or without a male (each $n = 15$). The presence of a male did not significantly affect female lifespan (15.5 ± 1.9 versus 14.3 ± 2.4 days; t-test, $P = 0.699$) or lifetime fecundity (3.9 ± 1.0 versus 4.5 ± 0.8 eggs; t-test, $P = 0.688$). The hatching success of eggs did not differ between treatments during the first (75% versus 69%; $\chi^2_1 = 0.27$, $P_{\alpha/2} = 0.303$) or second (75% versus 75%; $\chi^2_1 = 0.12$, $P_{\alpha/2} = 0.365$) week of the experiment, but was higher among females kept with a male during the third week (100% versus 33%; $\chi^2_1 = 5.14$, $P_{\alpha/2} = 0.041$). This suggests that females do not need to mate more than every two or three weeks to maintain full fecundity and fertility.

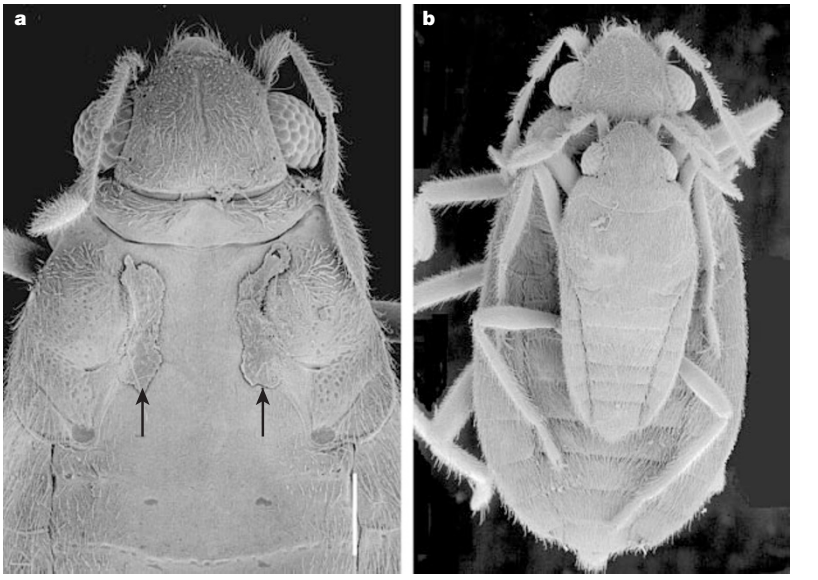

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Figure 1 Male Zeus bugs feed on females during mating. **a,** Females are equipped with a unique pair of dorsal glands, producing a secretion that upon drying creates two oblong, whitish patches (arrows). Scale bar, 0.2 mm. **b,** Males lack these glands, are much smaller than females (*P. disparata*; 1.2 as opposed to 2.0 mm), and ride adult females, as well as late-instar female nymphs, almost permanently without genital contact (mean mating duration in large laboratory populations; 8.2 ± 2.0 days, $n = 10$). During riding, the male mouthparts are located at the opening of the female dorsal glands. Adult sex ratio in the field is slightly male biased (1.2:1) and more than 95% of adult females carry a male on their back.

We have demonstrated a novel form of nuptial feeding, the evolution of which is unrelated to paternal investment. In conventional gift-giving species, males gain reproductive success by providing nuptial gifts[1]. In Zeus bugs, females might benefit from feeding and carrying males. Our results indicate that female gift-giving is not necessary to ensure a regular sperm supply[10], and that instead it might have evolved to reduce costs imposed by males, in the form of cannibalism, kleptoparasitism and other forms of interference.

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