

The extraordinary mating system of Zeus bugs (Heteroptera: Veliidae: *Phoreticovelia* sp.)*

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Abstract. Wingless female Zeus bugs (genus: *Phoreticovelia*) produce a secretion from dorsal glands that males feed upon when riding on females. This unique form of sex-role-reversed nuptial feeding may have set the stage for an unusual mating system. Here, we provide natural history details of the mating behaviour for two Zeus bug species. While these species have many mating behaviours in common, the wing morphs within species exhibit entirely different mating strategies. Adult wingless females are ridden permanently by adult wingless males. In the wild, adult sex-ratios among the wingless morph are male-biased; few unmounted adult females exist and many males instead ride immature females who also produce glandular secretions. In contrast, sex-ratios among the winged morph is not male-biased, sexual size dimorphism is less pronounced, females have no dorsal glands and are, consequently, not ridden by males. Field and laboratory observations show that mating is strongly assortative by wing morph. This assortment may allow evolutionary divergence between the two morphs. We discuss the implications of this mating system and suggest that it adds to those studies showing that sexually antagonistic coevolution can be a driver of mating system evolution.

Introduction

Much of our understanding of mating system evolution, and ultimately of sexual selection, comes from studying the natural history of mating systems that are extreme or unusual, in the sense that they represent outliers along some behavioural or morphological axis. Examples of such mating systems are bowerbirds (Frith and Frith 2004), taxa that undergo sex change (Munday *et al.* 2006), cooperatively breeding birds (Koenig and Dickinson 2004), lekking species (Höglund and Alatalo 1995), sex-role-reversed vertebrates (Andersson 2005), mole rats (Bennett and Faulkes 2000), guppies (Houde 1997) and sexually cannibalistic spiders (Elgar and Schneider 2004). The study of such mating systems is justified because they are likely to represent unusually clear manifestations of general evolutionary principles.

A newly discovered genus, *Phoreticovelia* (Infraorder: Gerromorpha; family: Veliidae; subfamily Microveliinae) (Polhemus and Polhemus 2000; Andersen and Weir 2001) has a remarkable, indeed probably unique, mating system (Arnqvist *et al.* 2003). Four species of Zeus bugs have been formally described on the basis of distinct differences in morphology: *Phoreticovelia rotunda* (Australian eastern seaboard); *P. disparata* (Queensland, Australia); *P. nigra* (Biak and Salawati, Irian Jaya); and *P. notophora* (Palau Islands). Like other gerromorphs, females are larger than males, but Zeus bugs are unusual because while there are both winged (macropterous) and non-winged (apterous) morphs – a common feature of semiaquatic hemipterans – these two morphs have distinct mating

systems. Recent observations of the non-winged (apterous) form of *P. disparata* in the laboratory (see Arnqvist *et al.* 2003) reveal an extraordinary mating system involving sex-role-reversed nuptial feeding.

In these small and elusive semiaquatic insects, apterous females, but not males, are equipped with a pair of dorsal glands that produce a wax-like secretion. Males are much smaller than females (male length = 1.0–1.2 mm, female length = 1.7–2.0 mm) and ride on the backs of females for extended periods in the laboratory. Riding males kleptoparasitise food items caught by females (Arnqvist *et al.* 2006), but single males are capable of capturing or scavenging food for themselves (personal observations). However, in *P. disparata*, males also feed on the glandular secretions produced by the females' dorsal glands, which are within reach of a male's mouthparts during his extended association with the female (Arnqvist *et al.* 2003). This unique case of sex-role-reversed nuptial feeding is made even more remarkable by the fact that female *P. disparata* start producing this secretion as juveniles (in their 4th or 5th larval instar), a time when adult males start riding these sexually immature females (based on laboratory observations). However, the winged (macropterous) females lack these glands and the sexes are more similar in size (male length = 1.7 mm, female length = 1.7–2.05 mm: Polhemus and Polhemus 2000; Andersen and Weir 2001).

Here, we report the first description of the habitat preferences and mating system of the two species of Australian Zeus

*This contribution is dedicated to the memory of Nils Møller Andersen, whose pioneering work on the biology and systematics of semiaquatic Heteroptera is a continual source of inspiration.

Table 1. Collection sites and the occurrence of different categories of Zeus bugs
 The collection sites were: Woobadda creek (road cross), Mulgrave river (Goldborough bridge), Henrietta Creek (at fusion with Goolagan creek), and Little Mulgrave River (upstream from bridge).
 WL, wingless; W, winged; +, refers to pairs

Species	Locality	Day or night catch	Site	WL male +		W male +		Single WL		WL male +		W male +		Single W		WL male +		
				WL female	WL female	WL female	WL female	male	female	male	female	male	female	male	female	male	female	male
<i>P. rotunda</i>	Woobadda Creek	D	A1	100	0	0	0	0	24	0	0	0	0	2	0	0	NA	
		D	A2	163	0	1	0	0	16	0	0	0	0	0	0	0	0	NA
		D	A3	64	0	0	0	0	17	0	0	0	0	0	0	0	0	NA
<i>P. disparata</i>	Mulgrave River	N		425	0	7	0	53	0	0	0	0	3	4	4	NA		
		N		0	0	0	0	0	0	0	0	0	0	61	73	NA		
<i>P. disparata</i>	Little Mulgrave River	D	A1	63	0	0	0	29	0	0	0	0	0	3	0	0	65	
		D	A2	23	0	0	0	15	0	0	0	0	0	3	1	1	18	
		D	A3	10	0	0	0	3	1	0	0	0	0	2	1	1	1	
		D	A4	38	0	0	0	10	0	0	0	1	0	7	3	8	7	
		D	A5	16	0	0	0	2	0	0	0	0	0	0	0	2	7	
		D	A6	40	1	0	0	4	0	0	0	0	0	6	2	2	4	
		D	A7	61	0	0	0	19	2	0	0	0	0	10	8	10	10	
		D	A8	12	0	0	0	4	0	0	0	0	0	1	1	4	4	
		D	A9	19	0	0	1	4	0	0	0	0	0	4	4	5	5	
		D	A10	126	0	0	0	14	1	0	0	2	0	19	21	48	48	
		D	B1	3	0	0	0	5	0	0	0	0	0	2	0	0	0	
D	B2	25	0	0	0	5	0	0	0	0	0	3	0	0	4			
D	B3	31	0	0	0	2	0	0	0	0	0	2	1	2	2			
D	B4	11	0	0	0	2	0	0	0	0	0	0	0	0	2			
D	B5	13	0	0	0	0	0	0	0	0	0	1	0	0	0			
D	B6	14	0	0	0	1	0	0	0	0	0	1	1	2	8			
D	C1	176	1	0	0	19	0	0	0	1	0	7	13	13	28			
D	C2	263	2	0	0	33	0	0	0	0	0	17	23	23	12			
D	D1	37	1	0	0	9	4	0	0	3	0	8	9	2	2			
N	E1	115	0	0	0	33	0	0	0	0	0	5	7	7	73			

bugs from four natural populations. Specifically, we document the location of day roosting sites and areas of night activity, adult sex-ratios, and the distribution and mating associations between the two wing morphs. We provide support for our observations of mating with a laboratory experiment that explores male riding behaviour in both species and wing morphs. Finally, we briefly discuss some of the general implications of the remarkable mating system of Zeus bugs.

Materials and methods

Field observations

During 13–16 September 2005, we conducted a quantitative field survey of *P. rotunda* and *P. disparata* in four different localities located in the eastern part of northern Queensland, Australia (one locality for *P. rotunda* and three for *P. disparata*: see Table 1). We made observations on their activity and habitat preferences and made collections by means of quantitative net sweeps, both during the day (roosting aggregations: see below) and during the night (open water surface). We determined sex and wing morph of all individuals caught. Especially detailed data were collected at one of the four sites (Little Mulgrave River), where we made day and night catches, and collected juvenile females and also recorded the presence or absence of male riding behaviour.

Male riding frequencies in the laboratory

To assess the proportion of time that females of the two wing morphs spend with males riding on their backs, we established replicated assays of *P. disparata* in tubs in the laboratory at 27°C and under a 14L:10D light cycle. Insufficient winged individuals were collected to conduct comparable assays for *P. rotunda*. For *P. disparata*, four males and four females were introduced into a tub (23 × 30 cm), which was filled with water (depth 4 cm) and provided with food and resting sites (balsawood and strips of paper). Five replicates contained only wingless (apterous) individuals, five contained only winged (macropterous) individuals and five contained two individuals of each sex and morph. We made regular spot samples during the following 48 h ($n = 13$; spot sample interval 1.25–15 h), recording the number of females that carried a male. The proportion of spot samples at which females carried a male is assumed to reflect the proportion of time spent carrying males. All proportions were arcsine-transformed before statistical analyses with parametric tests. Means are presented with their associated standard errors.

Results

Field observations

Habitat preferences

Zeus bugs inhabit streams and rivers, where they primarily occur in backwaters and slowly flowing sections (Polhemus and Polhemus 2000; Andersen and Weir 2001). The two species did not co-occur at any of the four sites sampled. Our observations show that *P. disparata* and *P. rotunda* are exclusively nocturnal. They were found skating across the water surface during the night, singly or in very loose aggregations, but only very rarely did they venture out on the open water during the day. Instead, they spent the daylight hours at communal roosting sites, where

they aggregated often in large numbers. Roosting sites for both species were typically pieces of partially submerged wood, such as logs and tree branches. They occurred along streamside margins, but the sites with the largest aggregations were located a few metres out in the stream. At roosting sites, the Zeus bugs were typically found sitting in clusters a few centimetres above the water line.

Aggregations at roosting sites contained anything from a few up to several hundred adults (mean number of adults per aggregation: 85 ± 21 , data for *P. disparata* in Little Mulgrave River) and sometimes large numbers of nymphs in addition (Table 1). Females prefer to lay their eggs in microcrevices in moist wood, and the presence of eggs and newly hatched offspring at roosting sites suggests that these are selected to provide a substrate with a structure and humidity suitable for oviposition. Our field data also indicate that *P. disparata* and *P. rotunda* share a common mating system: we failed to find any biologically or statistically significant differences between these closely related species (see below).

Winged and unwinged morphs

In general, individuals of the unwinged morph far outnumbered winged individuals (Table 1), a finding consistent with collected museum material from other populations (Polhemus and Polhemus 2000; Andersen and Weir 2001). The mean proportion of winged adults in roosting aggregations of *P. disparata* from the Little Mulgrave River was 0.08 (range 0–0.24). Nevertheless, a notable exception was the population in Henrietta Creek, in which only winged individuals were caught. In Little Mulgrave River, the proportion of winged adult *P. disparata* was lower in night catches than in day catches (0.04 v. 0.09 ; $\chi^2 = 9.94$, d.f. = 1, $P = 0.002$), suggesting that the winged morph is less active during the night.

Although the adult sex-ratio (number of males: number of females) in our catches differed across populations ($\chi^2 = 13.71$, d.f. = 3, $P = 0.003$) it was always male-biased, but significantly so only for *P. disparata* in Little Mulgrave River, which also supplied the largest sample size. The average sex-ratio for *P. rotunda* was 1.16 ($\chi^2 = 2.04$, d.f. = 1, $P = 0.153$), and for *P. disparata* 1.11 (Mulgrave River: $\chi^2 = 1.20$, d.f. = 1, $P = 0.272$), 1.20 (Henrietta Creek: $\chi^2 = 0.54$, d.f. = 1, $P = 0.463$) and 1.42 (Little Mulgrave River: $\chi^2 = 44.48$, d.f. = 1, $P < 0.001$). Interestingly, the adult sex-ratio of *P. disparata* in the Little Mulgrave River differed markedly between wing morphs ($\chi^2 = 10.06$, d.f. = 1, $P = 0.001$), and was significantly male-biased among wingless (1.47 ; $\chi^2 = 49.39$, d.f. = 1, $P < 0.001$) but not winged (0.95 ; $\chi^2 = 0.08$, d.f. = 1, $P = 0.778$) individuals.

Riding behaviour

Virtually all adult wingless females carried an adult male. The average proportion of adult wingless females with a riding male was 0.997 and 1.0 for *P. disparata* in Little Mulgrave River (day and night catches, respectively), 0.984 in Mulgrave River (day catch) and 0.998 for *P. rotunda* in Woobadda Creek (day catch). In stark contrast, very few winged females carried a male: the corresponding proportion was 0.079 and 0 (day and night catches, respectively) for *P. disparata* in Little Mulgrave River, and zero in all other populations. Thus, wingless females

spend virtually all of their time with a male on their back while winged females are only very rarely ridden by males.

Riding in Little Mulgrave River was strongly assortative according to wing morph. The proportion of winged males was only 0.5% among males riding wingless females but 46.7% among those riding winged females ($\chi^2 = 265.79$, d.f. = 1, Fisher's exact $P < 0.001$). Winged males were significantly under-represented as mates of wingless females ($\chi^2 = 53.30$, d.f. = 1, $P < 0.001$) but over-represented as mates of winged females ($\chi^2 = 37.78$, d.f. = 1, Fisher's exact $P < 0.001$), on the basis of their relative frequency in the population (6.4%). The strength of assortative mating by morph across all pairs was $r = 0.55$ when measured as a correlation coefficient and $\psi = 196.2$ when measured as an odds ratio. The proportion of wing morphs among males riding winged females was not significantly different from the proportion of wing morphs among single males ($\chi^2 = 1.08$, d.f. = 1, $P = 0.299$).

Our field data confirmed our laboratory observations of adult wingless *P. disparata* males riding juvenile females (Arnqvist *et al.* 2003). In the Little Mulgrave River, where the most detailed observations were made, 68% of all wingless males (total $n = 1618$) were found riding adult females, 13% were found alone and 19% were found riding fourth- and, in particular, fifth-instar juvenile females. The corresponding proportions for winged males (total $n = 110$) were 11%, 89% and 0% ($\chi^2 = 402.78$, d.f. = 2, $P < 0.001$). Clearly, the riding behaviour of wingless and winged males is very different. In contrast, we found no indications of marked differences in the mating system between wingless morphs of the two species. For example, the ratio of single males to males riding adult females in the field was 0.17 in *P. rotunda* (Woobadda Creek, day catch) and 0.18 in *P. disparata* (Little Mulgrave River, day catch) ($\chi^2 = 0.10$, d.f. = 1, $P = 0.756$).

Male riding frequencies in the laboratory

Among the same-morph replicates, winged *P. disparata* females spent, on average, $15 \pm 6.9\%$ and wingless females $79 \pm 5.3\%$ of their time with a male on their back (two-sample z -test: $z = 7.67$, $P < 0.001$). In the mixed-morph replicates, the corresponding proportions were $6 \pm 2.0\%$ and $92 \pm 4.9\%$ (paired t -test: $t = 11.5$, $P < 0.001$). Across all replicates, the proportion of time spent carrying a male tended to be higher during light than during dark conditions, although this was statistically significant only for the wingless morph ($11 \pm 4.3\%$ v. $9 \pm 3.1\%$ for the winged morph; paired t -test: $t = 0.6$, $P = 0.578$; and $88 \pm 3.9\%$ v. $79 \pm 4.8\%$ for the wingless morph; paired t -test: $t = 3.3$, $P < 0.009$). Remarkably, every observation of males riding females among the mixed-morph replicates involved females being ridden by a male of her own morph. This pattern was significantly different from random mating in both morphs (one-tailed Fisher's exact tests: $P = 0.038$ for winged females, $P < 0.001$ for unwinged females).

Discussion

It is clear from our observations that the wingless morphs of *P. rotunda* and *P. disparata* share a common mating system. However, the wingless and winged morphs of these species exhibit different mating systems. We first discuss the mating system of the more common wingless morph, then contrast this

with that of the winged morph and finally discuss some of the general implications of our findings.

The mating system of the wingless morph

The mating system of Zeus bugs is remarkable in several ways. Our field data show that adult female Zeus bugs spend all of their time carrying a riding male on their back. This is true both during the night, when they are active on the water surface, and when roosting during daytime. Earlier observations of laboratory cultures showed that the average riding duration is longer than a week (Arnqvist *et al.* 2003). The adult sex-ratio in natural populations is markedly male-biased and most adult males that were not riding adult females were riding late-instar female nymphs (some 20% of all adult males) that provide no immediate reproductive return. Our interpretation of these data is that single males have very little opportunity to find unoccupied adult females, and thus ride female nymphs and feed on their secretions. While this could simply represent a male foraging strategy, it is also likely to improve male mating success: when female nymphs moult into adulthood, males simply crawl from the cast larval skin onto the newly emerged adult female. This male habit of riding immature females may thus represent a form of adaptive premating guarding of a future mating opportunity. Analogous male strategies have been interpreted in a similar way in other invertebrates (e.g. butterflies: Deinert *et al.* 1994; spiders: Elgar 1998; crustaceans: Jormalainen 1998). Theory shows that such premating guarding can be adaptive for males under male-biased sex-ratios, when there are strong restrictions on the number of mating opportunities (e.g. Fromhage *et al.* 2005). In Zeus bugs, such male–female pair bonds could potentially last for life, a suggestion supported by the fact that females are occasionally found carrying a dead male on their back. It further implies that the turn-over rate of mates, and thus the level of polygamy, is low in the field. While it is extremely difficult to actually measure the realised mating rate of these small insects in the field, these data suggest that the mating system of the wingless morph may approach monogamy (i.e. the average number of lifetime mates may be as low as <1.5 on average).

The mating system of the winged morph

Sexual size dimorphism is much less pronounced in the winged morph (see Fig. 1) and the adult sex-ratio is not male-biased. Furthermore, females of the winged morph are not ridden by males for extended periods, and male–female pair bonds in the laboratory are relatively brief. These observations suggest that there is far greater opportunity for both sexes to mate with multiple partners, although whether this happens in natural populations is unknown. Thus, the mating system of the winged morph may approximate scramble competition polygyny (see Arnqvist 1997), as observed in most semiaquatic bugs. The fact that the two wing morphs differ so dramatically in their mating systems may have important implications for their relative fitness and this may thus, indirectly, affect their dispersal and colonisation. As proposed for other insects, such differences in life history may allow for both colonisation and reproduction to be enhanced by the partitioning of these functions between the two adult wing forms (Roff and Fairbairn 1991; Denno and Peterson 2000).

Assortative mating by wing morph

Mating by Zeus bugs in the field was strongly assortative by wing morph. Earlier studies report no assortative mating by wing morph in other semiaquatic insects (Fairbairn 1988; Arnqvist et al. 1996; Amano and Hayashi 1998) and we are unaware of any previous example of such strong homogamy by wing morph in any insect. Our field data suggested that this is not a result of differences in habitat preference between morphs, as confirmed by the fact that assortative mating was also observed in the laboratory. Instead, the mating experiment reported here revealed the mechanism involved in assortative mating. When a wingless male encounters a wingless female he remains on her back, feeding from her glandular secretion. Winged males, however, do not remain on the back of their mates. This is possibly due to their larger size (Fig. 1): food provided by females may be insufficient and/or they may be unable to secure a firm grip on her back. Consequently, wingless females will pair almost exclusively with wingless males. In contrast, winged females have no dorsal glands, and cannot feed their mates, and neither winged nor wingless males ride on their back. However, most wingless males are riding wingless or juvenile females, so the frequency of winged males is relatively high in the pool of unpaired males. Thus, winged males will be

over-represented as mates of winged females, leading to the assortment seen.

The strong assortative mating observed has two general consequences. First, assuming that wing morph is at least partly genetically determined, as is true for related taxa (e.g. Spence 1989), assortative mating will promote genetic variation for wing dimorphism (Crow and Felsenstein 1968). Second, it will allow for selection to build up considerable linkage disequilibrium between alleles coding for wing morph and those coding for any life-history traits that confer high fitness in the particular wing morph with which they are associated. For example, genes for wing morph and male body size may become genetically correlated. We note that this process captures the spirit of some recent models of sympatric speciation (e.g. Dieckmann and Doebeli 1999). Although the winged and wingless morph are indeed likely to have distinct life histories (Spence 1989; Spence and Andersen 1994), it is unlikely that even the high degree of assortative mating seen in Zeus bugs is sufficient to actually generate sympatric speciation into a winged and a wingless species (see Bolnick 2004). Our discovery of a purely winged population of *P. disparata* is interesting in this context, but it is worth noting that all four species in this genus exhibit both wing morphs (Polhemus and Polhemus 2000; Andersen and Weir 2001).

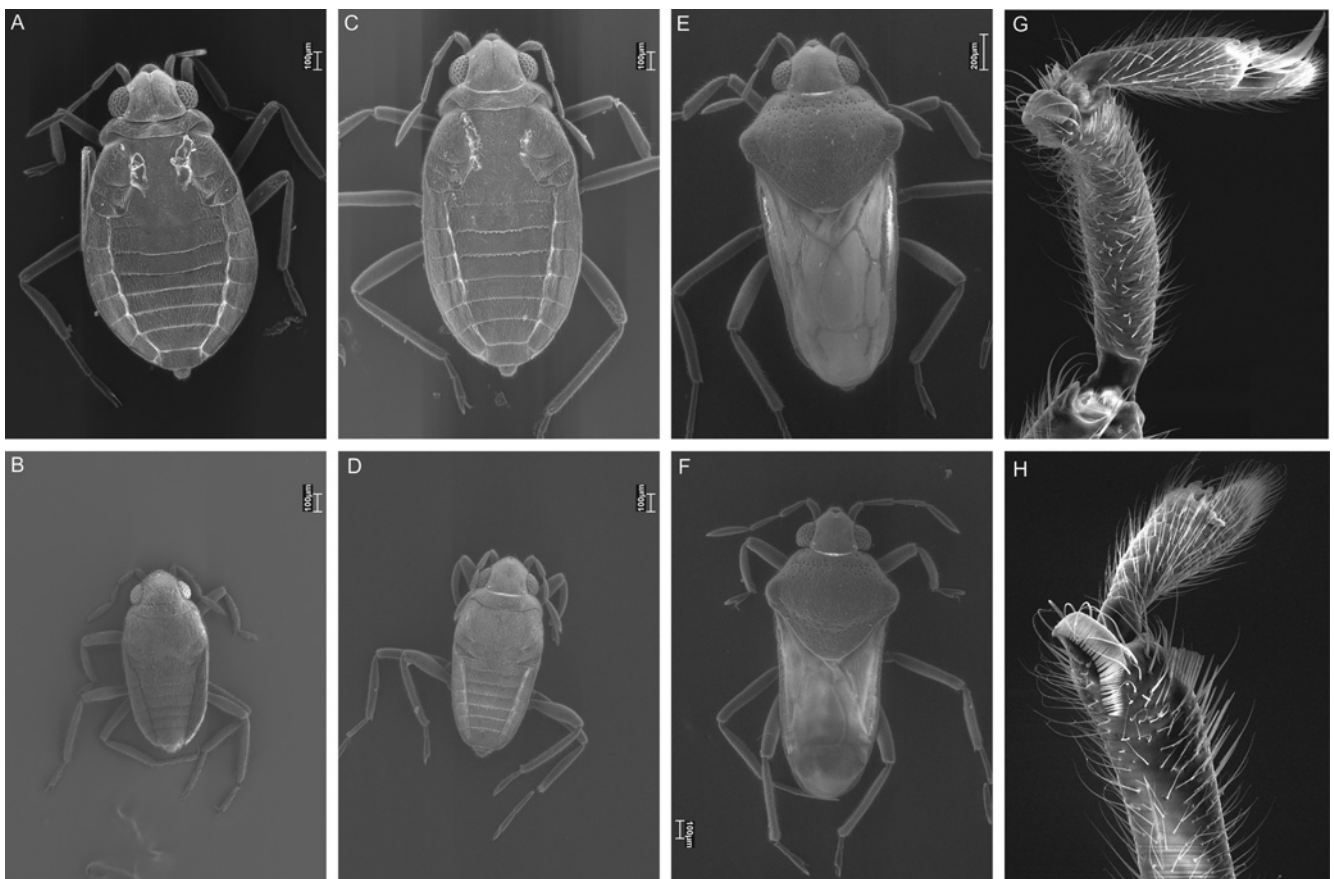


Fig. 1. Scanning electronic micrographs of *P. rotunda* (A, wingless female; B, wingless male) and *P. disparata* (C, wingless female; D, wingless male; E, winged female; F, winged male). Note the two patches of dried glandular secretions on the dorsum of wingless females, the absence of such patches in the winged female and the less pronounced sexual size dimorphism in the winged morph. Illustrated is also the male grasping comb, located at the tip of the fore tibia (*P. disparata*: G, winged male; H, wingless male).

The evolution of Zeus bug mating systems

The most puzzling aspect of the Zeus bug mating system is that adult and late-instar juvenile wingless females apparently produce nourishment for riding males. This sex-role-reversed nuptial feeding may have facilitated the extreme mating system of the wingless morph. Why, then, do females spend energy continually feeding their riding males? Zeus bugs live in dense populations with male-biased adult sex-ratios, and previous experiments indicate that females can store viable sperm for several weeks (Arnqvist *et al.* 2003). Thus, it seems unlikely that males represent a valuable insurance against a shortage of viable sperm for females. Females do not need to mate frequently to acquire sufficient sperm, and the abundance of males in the field suggests that females have little difficulty in replenishing their sperm supplies.

Several facts suggest that females may produce glandular secretions to minimise direct costs imposed by riding males. First, males commonly kleptoparasitise prey items caught by females (Arnqvist *et al.* 2006). Second, scarring of females in the region where the male mouthparts are held during riding indicate that riding males may, remarkably, occasionally bite females (authors' unpubl. obs.). Intense competition among male Zeus bugs for mating opportunities may have favoured the evolution of continuous mate guarding, a strategy that is costly to females (Parker 1979; Arnqvist and Rowe 2005). Provided that the glandular secretion is not too costly for females to produce, it may represent a counter-adaptation by which females minimise harm imposed by riding males. We note that the presence of a grasping comb on the forelegs (Fig. 1), in combination with small body size, makes it possible for males to achieve a very firm attachment to females (Polhemus and Polhemus 2000; Andersen and Weir 2001). Dislodging males, rather than feeding them, may be both difficult and futile given the presence of large numbers of single males in the population. The close timing between gland production and when males start riding females (during the fourth larval instar) and the fact that adult females produce gland secretions only when ridden by males (Arnqvist *et al.* 2003) are both consistent with the idea that the glandular secretion is a counter-adaptation to the costs of hosting riding males.

Our interpretation assumes intense male–male reproductive competition, as a result of the male-biased adult sex-ratio. We suggest that the biased sex-ratio is a direct consequence of the extreme sexual size dimorphism of wingless Zeus bugs: male bodyweight is ~20% that of females, egg–adult development time is much shorter in males than in females (authors' unpubl. obs.), and thus juvenile mortality in the field may be lower among males than females. Significantly, there is no adult sex-ratio bias in the winged morph, where sexual dimorphism is also much less pronounced (Fig. 1).

Our view of mating system evolution has been much influenced by the seminal paper by Emlen and Oring (1977), who suggested that ecological factors dictate the spatial and temporal pattern of male–female associations. The extant mating system then sets the stage for the dynamics of sexual selection within any given species (see Shuster and Wade 2003). Our understanding of the Zeus bug mating system suggests a quite different mode of mating system evolution. The key traits gen-

erating this mating system (kleptoparasitic male strategies that are costly for females and nuptial feeding by females as a counter-adaptation) seem to be the direct result of sexually antagonistic coevolution (*sensu* Rice 1996). The evolution of this extraordinary mating system would then be the result of intrinsic sexual selection rather than changes in extrinsic factors. Our study of Zeus bugs thus adds to a growing number of examples of a reversal of the order of cause and effect in mating system evolution, such that sexual selection may be a major driver, rather than a consequence, of mating system evolution (Arnqvist and Rowe 2005).

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