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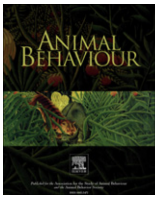

Extreme cost of male riding behaviour for juvenile females of the Zeus bug

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Precopulatory male mate guarding is predicted to occur close to the female's fertile period. However, in many species mate guarding commences when females are juveniles and may be several moults from sexual maturity. Such behaviour is inconsistent with the above prediction. In the Zeus bug, *Phoreticovelia disparata*, sexual size dimorphism is very pronounced and adult males commence riding on the backs of juvenile fourth-instar females. Males derive direct benefits from this association but the fitness consequences of precopulatory male riding behaviour for females are unknown. We investigated the effect of male presence during juvenile development for female Zeus bugs. We found a dramatic cost of male riding for females allocated a mate from the fourth instar: they were less likely to survive to adulthood and had substantially reduced adult longevity. These costs were significantly reduced for females allocated a mate during their fifth instar or as adults. We found no evidence that male presence affected female development time, adult size, body shape or the number of melanized dorsal scars present on their abdomen. Our study indicates that adult females and older juvenile females (fifth instar) are adapted to bear the costs imposed by riding males but that sexual conflict is likely to be intense between males and fourth-instar females. We suggest that the Zeus bug mating system originates from both sexes striving to make the best of a bad job: males ride immature females in the absence of unguarded adult females and females permit riding males as a form of convenience polyandry.

Male mate guarding, where males attempt to monopolize females pre- and postcopulation in order to maximize their fertilization success, is prevalent throughout the animal kingdom (Alcock 1991; Jormalainen 1998; Cooper & Telford 2000; Fuentes 2002; Shine 2003; Arakaki et al. 2004; Bochkov & O'Connor 2005; Todd et al. 2005; Yamanoi et al. 2006; Titelman et al. 2007; Oku 2009). The theoretical basis for the evolution and maintenance of a male guarding strategy, initially developed by Parker (1974) and Grafen & Ridley (1983), has been reviewed extensively (Parker 1974; Grafen & Ridley 1983; Alcock 1994; Tsubaki et al. 1994; Hardling et al. 2001; Simmons 2001; Fromhage et al. 2005; Kokko & Morrell 2005; Kokko & Rankin 2006). Precopulatory guarding is predicted when the female fertilization window is short, when females mate once only, or when there is limited (or no) capacity for sperm storage (Parker 1974; Grafen & Ridley 1983). In contrast, postcopulatory mate guarding is expected in species where females mate multiply and thus remain receptive to future mates following mating (Parker 1974; Grafen & Ridley 1983; Alcock 1994). Within a population, the intensity and duration of mate guarding are predicted to vary with season, density, sex ratio, the degree of female faithfulness or variation in female quality (Parker 1974; Alcock 1994; Hardling et al. 2001; Fromhage et al. 2005; Kokko & Morrell 2005; Kokko & Rankin 2006). Guarding is predicted to be for shorter durations or nonexistent when the cost–benefit ratio to males is high (Alcock 1994).

Typically, empirical studies that seek to explore the maintenance of male guarding behaviour have focused on its relative costs and benefits in situations where adult males guard adult females. Some of the most compelling evidence derives from studies of invertebrates. From the males' perspective, the primary benefit of guarding is that they increase their paternity share either through ensuring mating and reducing a female's access to future partners and/or by increasing the amount of sperm they transfer during extended or multiple copulations (Tsubaki et al. 1994; Campbell & Fairbairn 2001; Hosokawa & Suzuki 2001; Zhu & Tanaka 2002; Wynn & Vahed 2004). However, guarding is not without its costs. Guarding males may have a reduced feeding rate (Robinson & Doyle 1985; Sparkes et al. 1996), increased energy expenditure (Jormalainen & Merilaita 1993; Watson et al. 1998; Plaistow et al. 2003; Benesh et al. 2007), limited mating opportunities (Jormalainen et al. 1994; Jormalainen 1998; Titelman et al. 2007; Cothran 2008) and a greater risk of predation (Ward 1986; Dick et al. 1995;

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Elgar & Fahey 1996; Cothran 2004) or injury (Benesh et al. 2007). From the females' perspective, the presence of a male ensures fertilization which may be advantageous if access to males limits female reproductive success. However, females frequently incur substantial costs as a result of male mate guarding. Indirectly, male guarding behaviour may limit their choice of mates. More generally, it may be associated with direct costs such as decreased development or survival (Jormalainen et al. 2001; Wedell et al. 2006), increased energetic requirements (Watson et al. 1998) and increased risk of predation (Arnqvist 1989; Rowe 1994; Cothran 2004). At the extreme, males of some species actually cannibalize their females (Ward 1986; Dick et al. 1993; Dick 1995). In many species, it is suggested that females tolerate male presence because guarding males shield females from costly harassment from other males (Rowe 1994; Amano & Hayashi 1998; Watson et al. 1998). The magnitude of such costs can vary with sex ratio and population density and females may tolerate male guarding behaviour under certain conditions as a way of reducing them (Arnqvist 1992).

Typically, adult males guard adult females, but many studies of invertebrates reveal that precopulatory mate guarding commences when females are juveniles and may be several moults from achieving sexual maturity (Slooten & Lambert 1983; Burton 1985; Boxshall 1990; Evstigneeva 1993; Ritchie et al. 1996; Durbaum 1997; Fiers 1998; Jormalainen 1998; Thiel 2002; Zhu & Tanaka 2002; Arakaki et al. 2004; Bel-Venner & Venner 2006; Oku 2009). Unless a male is able to monopolize the female until she reaches sexually maturity, such behaviour is inconsistent with the prediction that, to optimize their mating rate, males should guard close to the female's fertile period (Parker 1974; Grafen & Ridley 1983). Limited evidence suggests that, if provided with the opportunity, males guarding very young juvenile females will switch between developmental stages, preferring to guard the one closest to sexual maturation (Burton 1985; Evstigneeva 1993). From a juvenile female's perspective, having a guarding male is likely to be costly, particularly for those species where a male attaches himself physically or rides on the back of a relatively smaller female. These costs may ultimately affect female development, survival and reproductive output. To our knowledge, no study where males guard during the early female juvenile phase has assessed experimentally the costs of male associations with juvenile females on female development and survival through to the reproductive phase of the adult lifecycle.

ZEUS BUGS

In the semiaquatic Zeus bug, *Phoreticovelia disparata*, sexual size dimorphism is very pronounced (Polhemus & Polhemus 2000; Andersen & Weir 2001): adult males are approximately 60% the length of adult females, 62% the length of fifth-instar juvenile females and 75% that of fourth-instar juvenile females (T. M. Jones, unpublished data). Zeus bugs are gregarious and the adult sex ratio is distinctly male biased (Arnqvist et al. 2007). Adult males ride on the backs of females and such pre- and postmating associations may last several days (Arnqvist et al. 2007). Intriguingly, adult males commence riding on the backs of juvenile fourth-instar females and while they can stay on their female even during moulting it is also possible that they will leave prior to the female reaching sexual maturity (Arnqvist et al. 2007). Regardless, males derive direct benefits from such associations with females. From the fourth instar, females are equipped with a pair of dorsal glands that produce a wax-like secretion (Andersen & Weir 2001; Arnqvist et al. 2003) that males feed from when riding (Arnqvist et al. 2003). Riding males also kleptoparasitize prey items captured by their mates (Arnqvist et al. 2006). However, the fitness consequences of precopulatory male riding behaviour for juvenile and adult females are unknown. Females can store sperm for up to 3 weeks (Arnqvist et al. 2003) and, as natural populations are very dense and show a male-biased sex ratio (Arnqvist et al. 2007), it is unlikely that guarding males represent a valuable insurance against a shortage of viable sperm. Instead, several lines of evidence suggest that there may be costs associated with male riding behaviour and that these are likely to vary between juvenile and adult females. First, approximately 70% of females initially struggle violently when males attempt to ride them (T. M. Jones, personal observations). Second, the relative energetic costs of carrying a male are likely to be highest for the smallest fourth-instar females and least for adult females. Third, adult females bear a varying number of melanized dorsal scars on their meso- and pronotum near where a male's proboscis is placed when riding and also have a pronounced body depression in the location where males ride that varies dramatically across adult females (Arnqvist et al. 2003). How this originates, whether it restricts egg production and storage and whether it is male imposed are unknown.

We investigated the effect of male presence on female development, survival and morphology by rearing individual juvenile females from the third instar through to adulthood with or without riding males for all or part of their lives. We predicted that the effects of bearing a male should be highest for females reared with a male from the fourth instar as the relative difference in size between the sexes during this phase of the female life cycle is at its smallest and/or because these females have also spent the longest duration bearing the potential costs of a riding male. We further predict that, if males are responsible for the observed female dorsal depression and scarring, these should be least pronounced in females allocated a male once they had reached the adult stage and most pronounced in females allocated a male from the fourth instar through to the adult stage.

METHODS

Zeus bugs were collected in Little Mulgrave River, Queensland, Australia (downstream from the Mulgrave River) and were brought into the laboratory to form a stock population. Bugs were maintained in aerated 30 × 40 cm tanks (water depth 10 cm), provided with polystyrene blocks and strips of balsa wood (as resting and oviposition sites) and fed ad libitum food (frozen cricket nymphs, *Acheta domesticus*, and adult *Drosophila melanogaster*). All Zeus bugs used in the experiment were of the apterous morph (Andersen & Weir 2001).

Juvenile Female Development and Survival

To explore the effect of the presence of a riding male on juvenile female development and survival, we selected at random 179 third-instar females from our stock population (between 300 and 500 individuals) and isolated them individually in cups (water depth 3 cm). Each cup was provided with a strip of balsa wood (2 × 1 cm) as a resting and oviposition site and females were given a single cricket nymph or adult *Drosophila* every other day. Females were then immediately assigned to one of six treatment groups that varied in the stage when a female was first allocated an adult male and how long after moult the male was introduced (Table 1). For each developmental stage, we introduced males either 2 or 4 days after the female had moulted; this procedure allowed us to disentangle the relative importance of the total duration of time a female spent with a male and the number of moults a female spent with a male. Every day, we recorded whether females were still alive or had moulted until they had completed their final moult from the fifth instar to an adult. If a male died during the trial, he was replaced with a new male from the stock population.

Table 1
Sample sizes and mean (SE) development time and scarring for the six female treatment groups

	Instar male introduced					
	Fourth		Fifth		Adult	
Days following moult	2	4	2	4	2	4
Number of third-instar females	35	31	22	28	33	30
Number of females surviving to adulthood	11	12	20	24	28	30
Days between fourth instar and adulthood	13.5 (0.64)	14.9 (0.39)	14.2 (0.44)	14.0 (0.36)	14.2 (0.37)	14.1 (0.44)
Number of dorsal scars	29.4 (8.47)	19.1 (6.43)	20.5 (5.07)	36.4 (4.90)	23.0 (6.23)	29.9 (5.35)

Female Morphology, Dorsal Scarring and Dorsal Shape

To assess male effects on the degree of scarring and the shape of a female's dorsal depression, we selected at random eight adult females per treatment group that had survived for 8 days as adults and preserved them in 70% alcohol. To explore whether male presence resulted in variation in the shape of the female dorsal depression, we first took casts of the dorsum of each female using a Blu-tack cast (Bostik, Helsingborg, Sweden). We then recorded a set of landmarks (mean $= 12.6 \pm 0.29$) from each cast, taken along the midline of the body from the base of the abdomen to the thorax, using a digitizing tablet (Summasketch III, GTCO CalComp, Inc., Scottsdale, AZ, U.S.A.) placed under a side-mounted camera lucida attached to a dissecting microscope (Leica MZ8, Leica Microsystems, Wetzlar, Germany). Each set of landmarks was first standardized in location and size, by anchoring all curves to $[x,y]$ 0,0 for the first point and 1,0 for the last point, using the software GRF-ND (Slice 1999). Variation in the shape of the dorsum was then parameterized by, for each individual, first fitting a conventional sixth-degree polynomial regression (forced through the origin) to the curve describing the dorsum. Variation in the partial regression coefficients of this simple open curve then reflects variance in the shape of the dorsum (Rohlf 1992). We tested for male effects using a MANCOVA with the six regression coefficients as response variables, the instar a male was introduced to a female (fourth, fifth, adult) and the number of days (2 days, 4 days) following her moult on which a male was introduced as factors and total length of the outline as a covariate.

To quantify the degree of dorsal scarring, we removed the dorsal body surface (i.e. the tergum) of each female and viewed it under a stereomicroscope (magnification ×6). To maximize contrast, we illuminated samples from underneath. For each female, we summed the number of scars present on the prothorax, the mesothorax and the first abdominal tergite. There was a strong correlation between the number of scars present in each of these regions (prothorax and mesothorax: $r_S = 0.56$, $P < 0.001$; prothorax and first tergite: $r_S = 0.38$, $P = 0.008$; mesothorax and first tergite: $r_S = 0.67$, $P < 0.001$). We also measured female body length (from the top of the mesonotum to the last abdominal tergite) as a measure of size, using the morphometric set-up described above.

Adult Female Survival

Upon reaching adulthood, all surviving experimental females were isolated individually in cups (see above) and then divided into two treatment groups that varied in their access to males (females in one group were provided with constant access to males; females in the second group were provided with males only for a 3-day period every week to ensure that they had sufficient sperm to fertilize their eggs). Females were maintained in this manner until their natural death and every 3 days the number of eggs laid on the oviposition substrate was recorded. Following their death, we dissected each female and recorded the number of eggs remaining in her abdomen.

Statistics

All data (except for those concerning dorsal depression) were analysed using JMP version 7.0.2 (SAS Institute Inc., Cary, NC, U.S.A.). The sequential Bonferroni procedure was applied to all post hoc tests to correct for multiple comparisons (Rice 1989). Differences in sample size across the six treatments arise as a result of either early misidentification of the juvenile stage and thus a male was added at the wrong instar (particularly between fourth- and fifth-instar females) or misidentification of a male as a female. Four females (adult, 2 days = 1 female; adult, 4 days = 1 female; fourth instar, 2 days = 2 females) were discarded from morphological analyses as their cuticle was too damaged to assess. Only four females from the stock population commenced oviposition, suggesting that the oviposition sites we provided were inappropriate. The total number of eggs remaining in the female's abdomen following death was instead used in the analysis of survival to control for potential differences in reproductive investment between females.

RESULTS

Juvenile Female Development and Survival

The number of days between the fourth instar and adult moults was comparable regardless of the stage of the female life cycle a male was introduced (effect of instar: $F_{2,117} = 0.03$, $P = 0.97$; days following moult: $F_{1,117} = 0.97$, $P = 0.33$; interaction between instar and days following moult: $F_{2,117} = 1.24$, $P = 0.29$; Table 1).

There was a significant effect of male presence on the likelihood of nymph survival (nominal logistic model: $\chi^2_4 = 56.17$, $P < 0.0001$; Fig. 1). Females allocated a mate in their fourth instar were significantly less likely to survive to the adult stage of the life cycle than

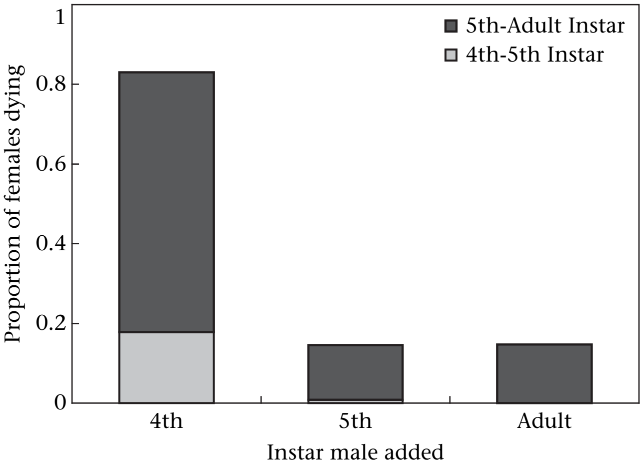

Figure 1. Proportion of female nymphs dying during fourth and fifth instars across the three treatments.

females allocated a male in their fifth or adult instars; there was no apparent difference between the latter groups of females. The number of days following a moult that the male was introduced had no impact on female nymph survival ($\chi^2_2 = 0.08$, $P = 0.96$) nor was there any interaction between the instar and day a male was introduced ($\chi^2_4 = 0.59$, $P = 0.96$).

Female Morphology, Dorsal Scarring and Dorsal Shape

Adult female length (mean ± SD length of fourth-instar females: 1.450 ± 0.01 mm; fifth-instar females: 1.472 ± 0.01; adult females: 1.436 ± 0.01; $N = 42$ females) was comparable regardless of the stage of the female life cycle a male was introduced (effect of instar: $F_{2,34} = 2.85$, $P = 0.07$; days following moult: $F_{1,34} = 2.46$, $P = 0.13$; interaction between instar and days following moult: $F_{2,34} = 0.55$, $P = 0.59$) and was unrelated to the number of developmental days between the fourth instar and the final adult moult ($F_{1,34} = 2.77$, $P = 0.11$).

The variation in the total number of dorsal scars observed on a female was not explained by the instar a male was introduced (mean ± SE number of scars = 26.16 ± 2.48; $F_{2,33} = 0.89$, $P = 0.42$), the number of days following a moult the male was introduced ($F_{1,33} = 0.49$, $P = 0.49$), the interaction between instar and days following a moult ($F_{2,33} = 2.57$, $P = 0.09$), the time taken to develop from the fourth instar to the adult stage ($F_{1,33} = 0.06$, $P = 0.80$) or to female body length ($F_{1,33} = 0.36$, $P = 0.55$).

The shape of the female dorsum was not significantly related to the instar when the male was introduced ($F_{12,64} = 0.45$, $P = 0.94$), the number of days following a moult the male was introduced ($F_{6,32} = 2.21$, $P = 0.15$) or to female body length ($F_{6,32} = 0.70$, $P = 0.65$).

Adult Female Survival

There was a significant effect of the instar when a male was introduced on adult female survival (Table 2, Fig. 2). Post hoc comparisons revealed that females that had a male added at the fourth instar survived for fewer days as adults than females with a male introduced at either the fifth instar (log-rank test: $\chi^2_1 = 9.19$, $P = 0.004$) or the adult stage of the life cycle (log-rank test: $\chi^2_1 = 28.05$, $P < 0.0003$). Survival for the latter two groups of females was comparable (log-rank test: $\chi^2_1 = 1.59$, $P = 0.21$). There was a positive relationship between the number of eggs stored in the female's abdomen and the number of days survived (β (SE) = 0.19 (0.04); Table 2). There was no effect on female survival of the number of days following a moult when a male was introduced or whether females had constant or limited access to males (Table 2). Furthermore, none of these factors interacted in their effects on adult female life span (Table 2).

Table 2
Parametric proportional hazard survival analysis exploring the effect of male presence and fecundity on female survival (see text)

Effect	*df*	χ^2	*P*
Instar male introduced (fourth, fifth, adult)	2	13.86	0.001
Days following moult (2, 4)	1	0.63	0.43
Male presence during adult life (constant, half-time)	1	0.26	0.61
Eggs remaining in female abdomen	1	21.36	<0.0001
Instar male introduced*Days following moult	2	0.35	0.84
Instar male introduced*Male presence during adult life	2	0.34	0.84
Days following moult*Male presence during adult life	1	0.1	0.94

Whole model: $\chi^2_{10} = 44.10$, $P < 0.0001$.

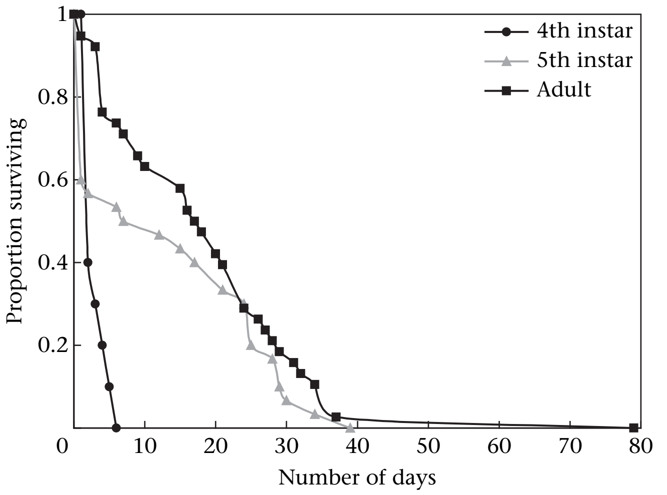

Figure 2. Adult female survival among females first exposed to males as fourth instar, fifth instar or as adults.

DISCUSSION

A thorough understanding of a mating system requires quantification of the economics of male–female interactions (Arnqvist & Rowe 2005). However, data on the costs and benefits of mate guarding to females are rare. Our study demonstrates a dramatic cost of male riding behaviour for young juvenile female Zeus bugs allocated a male: they were less likely to survive to their final adult moult and those that did reach the adult stage of the life cycle had substantially reduced adult longevity. Such costs were lower for females allocated a mate during their fifth juvenile instar or as adults. In Zeus bugs adult males commonly ride fourth-instar females in natural populations (Arnqvist et al. 2007), suggesting that the costs of male guarding to females are sizeable. However, we found no evidence that male presence affected female development times, adult size, body shape or the number of melanized dorsal scars present on their abdomen.

How and Why do Costs Arise for Fourth-instar Females?

The most likely explanation for the observed variation in survival across the three groups of females is that fourth-instar females experienced increased stress and energetic costs caused by the extended presence of males during their developmental period. Such costs could manifest themselves in at least five ways. First, during the fourth instar, juvenile females are only slightly larger than their riding adult male, so the relative energetic costs incurred during this period will be higher than for fifth instar and adult females which are considerably larger than their males. Second, one of the more costly components of bearing a riding male is the struggling period that occurs prior to riding; in the waterstrider *Aquarius remigis*, premating struggling behaviour was 126% more energetically costly than simply cruising along carrying a male (Watson et al. 1998). In our experiment, the number of struggling events was almost certainly correlated with the duration of exposure to males and thus will be highest for fourth-instar females. The energetic costs of struggling have not been quantified directly for *P. disparata*, but fourth-instar females can drown during the process (T. M. Jones, personal observation). Such an extreme form of male-imposed harm is unusual, but is known for other species including dung flies, *Sepsis cynipsea* (Muhlhauser & Blanckenhorn 2002), elephant seals, *Mirounga angustirostris* (Leboeuf & Mesnick 1991) and waterfowl (reviewed in McKinney et al. 1983; Arnqvist & Rowe

2005). Third, a potential cost incurred by Zeus bug females carrying a male is that they are likely to have experienced reduced levels of feeding because of male kleptoparasitic behaviour (Arnqvist et al. 2006) and such costs may be more severe for younger females. Fourth, fourth-instar females had a male present for two moults (compared to one for fifth instar and none for adult females). Upon moulting, the cuticle of the female is soft and initially unmelanized and the female is extremely vulnerable to cannibalism and male-imposed damage or stress (Dick et al. 1993; Dick 1995; Jormalainen et al. 2001). Fifth, female Zeus bugs (starting from the fourth instar) are equipped with a pair of dorsal glands that produce a secretion that males feed from when riding (Arnqvist et al. 2003). Because the presence of a male triggers production of this secretion (Arnqvist et al. 2003), any costs to females that result from producing this secretion are likely to be higher the earlier a female is ridden by a male. We note that observed costs imposed on females in the laboratory may be further exacerbated in the less benign field environment. In particular, the presence of a riding male may increase the risk of predation (Arnqvist 1989; Rowe 1994; Cothran 2004). Zeus bug females tend to stop struggling once additional males gather around suggesting that they are either reducing harassment or that struggling may increase the risk of attracting predatory species such as diving beetles.

What are the Benefits for Females?

Given the very high density of males and females in natural populations and the male-biased sex ratio (Arnqvist et al. 2007) it is very unlikely that females require males to ride for extended periods to ensure fertilization, particularly given that the number of eggs produced is very low (mean ± SE number of eggs per week $= 0.39 \pm 0.07$; this study; see also Arnqvist et al. 2003). It is possible that the presence of a riding male reduces harassment from other males (Rowe 1992; Arnqvist 1997; Amano & Hayashi 1998; Watson et al. 1998), although rival Zeus bug males are capable of copulating with an already paired female (T. M. Jones, personal observation). Furthermore, the costs of tolerating an existing riding male may be lower than those that would be associated with dislodging the current male (which would be rapidly replaced by another male).

Why do Males Ride Fourth-instar Females?

Theory predicts that precopulation associations are favoured as a means of monopolizing access to females until they are sexually receptive, rather than as a means of avoiding sperm competition (Simmons 2001). More particularly, mate guarding is expected when the window of female receptivity is short, females mate once only and there is little capacity for sperm storage (see references above). Male Zeus bugs may benefit in two different ways from riding young juvenile females. First, associating with a fourth-instar female Zeus bug may yield subsequent fertilization benefits to males, as they are able to continue guarding the female across successive moults. However, we suggest that such benefits are small as female Zeus bugs seem to mate multiply and because males lose mating opportunities during the 2 weeks it takes a fourth-instar female to reach adulthood. Second, males may gain direct benefits from riding young immature females through increased access to food via kleptoparasitism and/or glandular secretions and because they minimize energetic costs of locomotion. Such a parasitic strategy is further promoted by the male-biased adult sex ratio in natural populations (Arnqvist et al. 2007) which means that males derive benefits from riding juvenile females in spite of the reduced potential for mating. Indeed, mate switching almost certainly occurs when females are either feeding or more typically at roosting sites. Thus, riding a fourth-instar female allows males to be carried to a roosting site where they could potentially ‘trade up’ to a fifth or possibly sexually mature, but almost certainly mated, adult female. A similar strategy is seen in certain copepods where males guard juvenile females but given the opportunity will switch to older females which are closer to sexual maturation (Burton 1985).

Whether males or females determine the outcome of preriding struggles is unknown. Males bear a ‘grasping comb’ on their foreleg which is thought to facilitate grasping when they ride females, but its effectiveness is untested (Andersen & Weir 2001; Arnqvist et al. 2007). In some crustaceans, juvenile females have adaptations at the younger instars which actually facilitate male clasping behaviour (Fiers 1998). However, no related antigrasping female structure has been observed in Zeus bugs.

Zeus bugs show a truly remarkable mating system (Arnqvist et al. 2003, 2007). We have shown here that adult females and older juvenile females (fifth instar) seem well adapted to bear the costs imposed by a riding male (Arnqvist et al. 2006). In contrast, male riding behaviour is clearly very costly for young juvenile females and sexual conflict over male riding should be intense at this stage. We predict that this mating system may, in part, originate from both sexes striving to make the best of a bad job: males ride immature females in the absence of unguarded adult females and females allow males to ride and even provide them with glandular secretions as a form of convenience polyandry (sensu Thornhill & Alcock 1983).

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