



# Intrasexual competition and mate choice in assassin bugs with uniparental male and female care

LISA K. THOMAS & ANDREA MANICA

Department of Zoology, University of Cambridge

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Paternal care has the potential to lead to female-biased operational sex ratios and sex role reversal. Whereas this issue has been repeatedly investigated in fish, we present the first study on insects. We investigated two species of assassin bug: *Rhinocoris tristis*, which shows male care of eggs, and *Rhinocoris carmelita*, which shows female care of eggs. In both species, the potential reproductive rate of males exceeded that of females. Since the population sex ratio was unbiased and there was no difference in mortality rates between the sexes, we predicted that the operational sex ratio would be skewed in favour of males in both species and thus males would be the more competitive sex. Field and laboratory observations upheld this prediction, with males competing for females in both species. In *R. tristis*, males also competed for ownership of eggs, whereas females discriminated between males according to ownership of eggs. However, choosiness was not restricted to females in *R. tristis*. Observations suggested that *R. tristis* males discriminated between females according to their weight: heavier females, which were likely to oviposit sooner, were guarded for longer by males in a period of postcopulatory riding. We suggest that the primary function of postcopulatory riding is to prevent females from mating with conspecifics, thus reducing the possibility of sperm competition. This behaviour might also be an important prerequisite for the evolution of male care.

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The importance of parental care in the determination of sex roles and the intensity of sexual selection has long been recognized (Williams 1966). Trivers (1972) clarified the nature of the association, defining parental investment and arguing that relative parental investment controls both the degree of intrasexual competition and the intensity of sexual selection. His theory suggests that individuals of the sex with a higher investment will become the limiting factor, leading to choosiness; on the other hand, the sex investing less will start competing for access to the limiting sex.

This theory was modified when researchers realized that factors other than parental investment, such as relative survival, differences in the costs of competition and the adult sex ratio, can also have an effect. Emlen & Oring (1977) suggested that the ratio of sexually receptive males to females (operational sex ratio, OSR) is the best predictor of interspecific patterns of competition. Researches have

argued that this modification does not invalidate Trivers' original suggestion because, although many variables affect the OSR, relative parental investment is probably the most important contributing factor (Clutton-Brock & Vincent 1991; Clutton-Brock & Parker 1992). Because this is the case, potential reproductive rates of males and females (the maximum number of independent offspring produced by males and females per unit time), as a measure of the OSR, may be used to predict patterns of competition between the sexes. Thus, the sex with the higher potential reproductive rate should compete more intensely for mates than the sex with the lower potential reproductive rate (Clutton-Brock & Vincent 1991), although large sex differences in mortality patterns can still override the predicted effect of potential reproductive rate and OSR on the direction of sexual selection (Kokko & Monaghan 2001).

Potential reproductive rates can also be used as a measure of the OSR to predict choosiness. However, choosiness may also depend on other factors, such as variance in mate quality (Johnstone et al. 1996). Therefore, in some species, where male and female potential reproductive rates are similar, such as the Eurasian dotterel, *Charadrius*

Correspondence: A. Manica, Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: [am315@cam.ac.uk](mailto:am315@cam.ac.uk)).

*morinellus*, males are both the more competitive and the more choosy sex (Owens & Thompson 1994).

Although most species with maternal care are characterized by higher relative female investment and thus show the typical patterns of male competition and female choice, relative investment is more variable within species displaying paternal care. For example, in the pipefish, *Syngnathus typhle* and *Nerophis ophidion*, paternal brooding is accompanied by higher relative male investment and role reversal (Vincent et al. 1992). In others, such as the three-spined stickleback, *Gasterosteus aculeatus*, female investment outweighs that of males despite female emancipation from care and thus the typical sex roles are assumed (Kynard 1979). The potential for dissociation between the care-giving sex and the sex with the higher levels of investment means that species with paternal care provide a valuable insight into the role of parental investment in determining patterns of competition.

Work on potential reproductive rates in insects has mostly concentrated on the effect of parental investment through nuptial feeding (e.g. Gwynne 1990; Simmons 1992). For example, in katydids, males provide the female with a nutritious spermatophore during courtship. When food is plentiful, this species show the traditional sex roles during courtship, but a reversal occurs when food is scarce, when females compete for access to mates and males become choosy (Gwynne & Simmons 1990; Simmons & Bailey 1990). Much less attention has been devoted to the effect of parental care on sexual selection. In giant water bugs, *Belostoma flamineum*, where the male carries the eggs on its back, the operational sex ratio is female biased for the first part of the breeding season (Kruse 1990), leading to sex role reversal (Smith 1979). However, to our knowledge, our work is the first to compare two congeneric species with opposite parental care patterns.

*Rhinocoris tristis* and *Rhinocoris carmelita* are two species of assassin bugs in the subfamily Harpactorinae. They occur in sub-Saharan Africa and are both polyphagous predators. *Rhinocoris tristis* is usually found at high density and is associated with the legume *Stylosanthes guinaensis*, probably because of the large number of prey attracted by the flowers of this species (Thomas 1994; Thomas & Manica 2003). However, *R. tristis* can be successfully reared in captivity without any *Stylosanthes*, and specimens are often found on other species of plants within *Stylosanthes* patches (Thomas & Manica 2003). *Rhinocoris carmelita*, on the other hand, does not show any association with a specific species of plant, and it prefers low herbs or woody plants (Thomas 1994). Male *R. tristis* guard the eggs and parental care lasts for 15–43 days, depending on the brood incubation period (Thomas 1994). Guarding males are simultaneously polygynous, mating and receiving eggs from several females in one brood (defined as all the eggs defended by a male, usually forming a cohesive clump). In contrast, *R. carmelita* males are usually not present at oviposition and females guard their own eggs. Egg mortality in both species occurs as a result of attacks by parasitic wasps and insect predators (Thomas 1994; Thomas & Manica 2003). Male *R. tristis* also cannibalize some of their own eggs to offset the energetic cost of care

(Thomas 1994; Thomas & Manica 2003). We investigated the effect of uniparental care on intrasexual competition and mate choice in the paternal *R. tristis* and the maternal *R. carmelita*.

## METHODS

### Field Studies

We carried out fieldwork on *R. tristis* at two sites in Uganda: Kawanda Research Station and Kabanyolo Agricultural Station, between February and September 1992. The site at Kawanda consisted of a plot of *Stylosanthes* (30 × 15 m) which was used for manipulations, and we monitored an unmanipulated population on a plot (10 × 2 m) at Kabanyolo. Work on *R. carmelita* was carried out at the Cocoa Research Institute at Tafo in Ghana between July and October 1993. We collected bugs from mixed herb vegetation around the station and monitored broods from two separate sites.

Adults were marked with a unique colour combination of correcting fluid (Tipp-Ex, Bic GmbH) along the dorsal abdomen. We monitored the position (using a grid reference ±0.5 m) and activity (feeding, mating, ovipositing, guarding) of individual insects daily between 0900 and 1700 hours. Each time we encountered a brood, we counted the eggs, and sketched a map with the position of each egg to monitor predation. Broods were subsequently monitored twice a day, at 0900 and 1700 hours. On each occasion, we recorded the presence of a guarding adult and the position of hatched and unhatched eggs. Brood take-overs (only seen in *R. tristis*) were recorded when an incoming male took over an existing brood and maintained ownership of the eggs until hatching. Monitoring was continued until all eggs had hatched or been destroyed by predators. After hatching was complete, we collected the brood for dissection under a microscope. Each egg was recorded on the map as successfully hatched (with a detached operculum), parasitized (with an intact operculum and either containing a parasitic wasp or with a wasp exit hole towards the egg base), cannibalized (egg empty with no visible damage) or lost through predation (see Thomas 1994 for a detailed description of each state). We never observed any other form of prehatching mortality (see also Thomas & Manica 2003), possibly because the male cannibalizes any eggs that fail to develop properly.

### Laboratory Studies

We carried out laboratory manipulations in Kawanda and Tafo at the same time as fieldwork. Adults were collected in the field and kept in cylindrical breeding cages (diameter 13.3 cm, height 23.5; Watkins and Doncaster: Economy Range Breeding Cage, Hawkhurst, U.K.) under natural light and temperature conditions. We also repeatedly imported *R. tristis* to Cambridge, U.K., between October 1992 and March 1994, where they were kept at 28°C with a 12:12 h light:dark regime. Laboratory conditions were similar to natural conditions. Bugs were fed

daily on *Drosophila*. Two uniform wooden canes (as used to straighten plants, ca. 20 cm long) were placed in each cage and the bugs readily accepted them for egg laying (Thomas & Manica 2003).

### Survival and Adult Sex Ratio

Adult survival was estimated from daily censuses. We measured the interval between the day on which an adult was marked and the day on which it was last seen. Individuals were included in the analysis only if they were seen on at least 5 separate days. Reliable estimates could be obtained only for *R. tristis*, owing to the low re-encounter rate for *R. carmelita*. To obtain adult sex ratios for the two species we counted and sexed all the individuals found in a 20-m<sup>2</sup> area in Kawanda, Kabanyolo and Tafo.

### Potential Reproductive Rates

For both species, we estimated the maximum rate of female offspring production by providing females with both males and unlimited *Drosophila* in the laboratory ( $N = 9$  replicates for *R. tristis*,  $N = 8$  for *R. carmelita*). We counted the eggs produced by each female each day for 16 days. Maximum reproductive rates for males were estimated from observations of matings between pairs in the laboratory ( $N = 10$ ).

Laboratory estimates of reproductive success for the caring sex do not take into account the cost of protecting the eggs from parasites. Field estimates, which would correct for this bias, could be obtained only for *R. tristis* during a period of intensive brood monitoring ( $N = 44$ ). This sort of monitoring could not be carried out for *R. carmelita*, since this species is found only at relatively low densities and we never found enough guarding specimens. Up to 11 batches of eggs may be added to an *R. tristis* brood in a single day. Therefore, we recorded the initial size of a new brood by individually mapping eggs on to paper. The opercula of these eggs were brushed with a weak solution of red food colouring. Colouring eggs has no effect on parasitism or cannibalism (Thomas 1994). As additional eggs were laid, we mapped their position and noted the date on which they were laid. Broods were monitored at 30-min intervals between 0900 and 1700 hours. Every 30 min, we recorded the following information: (1) the presence or absence of the guarding male (males were recorded as being present on any given day if they were within 5 cm of the brood for more than half the daily observations); (2) the presence, identity and behaviour of any females; (3) the number of eggs in the brood. The date of hatching of each egg was marked on the map. This process was continued until all eggs had hatched or been destroyed by predators.

### Competition

For *R. tristis*, we used field observations made during the period of intensive brood monitoring (as described above)

to assess the existence and extent of competition over mates in both sexes. In *R. carmelita*, low individual encounter rate did not permit field observation of competition. Therefore, we investigated competitive behaviour in the laboratory by observing male and female behaviour in groups with a 3:1 and 1:3 male:female sex ratio ( $N = 10$  for each sex ratio).

### Mate Choice

Individuals may choose mates on the basis of a large number of attributes but we considered only choice for mates of different weights. Weight seems a likely candidate for mate discrimination as it is linked to female fecundity and male competitive ability among many ectotherms (reviewed in Johnstone 1995). Ten pairs of each species were randomly formed from our laboratory populations and were housed in individual cages. Males and females were weighed immediately before the experiment. We observed pairs continuously until the male dismounted from the female's back and stopped trying to copulate. We examined the probability of attempted and successful mating, together with the relation between male and female weight and the duration of the pre-copulatory period, copulation and postcopulatory period.

### Female Choice and Male Competition

To investigate whether females prefer guarding males and whether males compete for females, we conducted a simultaneous choice experiment ( $N = 15$ ). We collected *R. tristis* males from the field at Kawanda and placed a single, nonguarding male and a gravid female together in a cage containing a single stem of *Stylosanthes*. After mating, the male was allowed to remain in the post-copulatory riding position for 1 h. After 1 h, a second male that was guarding eggs was introduced into the cage. We observed the behaviour of all three individuals until the female oviposited.

## RESULTS

### Survival and Adult Sex Ratio

Male *R. tristis* were seen in the field for a mean  $\pm$  SE of  $35.0 \pm 2.2$  days ( $N = 82$ ) compared with  $31.4 \pm 2.5$  days ( $N = 46$ ) for females, showing no sex difference in survival ( $t$  test:  $t_{126} = 1.01$ ,  $P = 0.24$ , power = 0.73 for an effect size of 5% at  $\alpha = 0.05$ ). There was no evidence that males suffered increased mortality during parental care: males that abandoned broods were no less likely to be re-encountered after desertion (19 of 35) than males that had not been guarding eggs (35 of 37;  $G$  test with Williams's correction:  $G_1 = 0.44$ ,  $P = 0.48$ ), suggesting that abandonment was the result of male decisions rather than predation. The sex ratio did not differ significantly from 1:1 for *R. tristis* (375 males versus 338 females;  $G_1 = 1.92$ ,  $P = 0.11$ , power = 0.99 for an effect size of 10% at  $\alpha = 0.05$ ) or *R. carmelita* (176 males versus 165

females;  $G_1 = 0.35$ ,  $P = 0.56$ , power = 0.96 for an effect size of 10% at  $\alpha = 0.05$ ).

### Potential Reproductive Rates

*Rhinocoris tristis* females produced a batch of eggs every 1–2 days for 16 days in the presence of males and unlimited food. This led to a mean oviposition rate  $\pm$  SE of  $3.7 \pm 0.5$  eggs/day ( $N = 9$ ), with a maximum rate of 10.8 eggs/day. On the other hand, *R. carmelita* produced  $5.1 \pm 0.6$  eggs/day ( $N = 8$ ), with a maximum of 8.1 eggs/day.

The average duration of mating in the laboratory was 7.15 h for *R. tristis* and 1.86 h for *R. carmelita*, but minimum times were 0.54 h and 0.27 h, respectively. *Rhinocoris tristis* males mated up to twice a day in the laboratory ( $\bar{X} \pm \text{SE} = 1.8 \pm 0.1$ ,  $N = 10$ ), but individuals in the field collected up to three batches of eggs ( $1.6 \pm 0.2$ ,  $N = 44$ ). This led to a mean potential reproductive rate  $\pm$  SE of  $47.0 \pm 7.3$  eggs/day ( $N = 10$ ) in the laboratory, and of  $23.4 \pm 10.3$  eggs/day ( $N = 44$ ) in the field (with a maximum potential rate of 112 eggs/day). Male *R. carmelita* mated up to twice a day in the laboratory ( $1.6 \pm 0.2$ ,  $N = 9$ ) and fertilized a mean of  $63.5 \pm 7.2$  eggs/day ( $N = 9$ , maximum = 92.6). Male potential reproductive rates were much higher than female potential reproductive rates in both *R. tristis* (field:  $t_9 = 5.92$ ,  $P < 0.001$ ; laboratory:  $t_{43} = 1.91$ ,  $P = 0.063$ ) and *R. carmelita* ( $t_8 = 8.08$ ,  $P < 0.001$ ).

### Competition

We observed *R. tristis* males competing for females in the field. On three occasions, a pair engaged in postcopulatory riding was attacked by a solitary nonguarding male, which attempted to dislodge the resident male. The riding male was successful in repelling the intruder on each attack.

In addition to competition over females, male competition for egg broods was also observed in the field and laboratory. Attempted take-overs of guarded broods were observed in 10.6% of broods (eight of 75) at Kabanyolo and 22.7% of broods (five of 22) at Kawanda. Successful take-overs were observed in 6.7% of broods (five of 75) at Kabanyolo and 9.1% of broods (two of 22) at Kawanda. During take-over of a guarded brood, the intruding male approached the eggs with antennae extended. The guarding male typically responded to the approach by reciprocally extending his own antennae and moving towards the intruder. If the two individuals came within a few centimetres of each other without the intruder backing off, one or both would raise their forelegs as if about to attack. This confrontation, which lasted from a few seconds to several minutes, often resulted in the intruder retreating. However, on a few occasions, escalation occurred and the two males locked together in a fight until one retreated or fell off the plant. The 'winner' took over the brood and resumed guarding behaviour.

On several occasions, two *R. tristis* females were observed ovipositing simultaneously in one male-guarded brood in the field. There was no evidence of any aggressive

behaviour between the females and hence no evidence for female competition over mates.

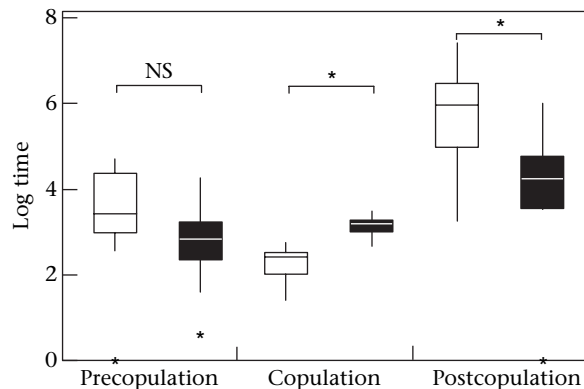
In *R. carmelita*, males also competed directly for females. For groups placed in cages with a 3:1 sex ratio, copulation between a pair was terminated by the approach and aggressive behaviour of the unpaired male on three of 10 occasions. On two occasions, the intruder copulated with the female after the original pair had separated. Females occasionally showed an aggressive posture towards copulating pairs in cages with a 1:3 sex ratio, but this was brief and never resulted in pair separations.

### Mate Choice

The two species differed in their mating behaviour: *R. carmelita* invested more time in copulation than *R. tristis*, whereas the reverse was true for postcopulatory riding (Fig. 1). The probability and duration of precopulatory riding, mating and postcopulatory riding were unrelated to male weight in *R. tristis* and unrelated to male or female weight in *R. carmelita* (Table 1). However, in *R. tristis*, copulation was more likely to occur between pairs with heavier females (Table 1). In addition, the duration of postcopulatory riding increased significantly with female weight (Spearman rank correlation:  $r_s = 0.89$ ,  $N = 10$ ,  $P = 0.007$ ; Table 1). Female weight was in turn related to the time until oviposition: heavier females oviposited sooner ( $r_s = -0.55$ ,  $N = 28$ ,  $P = 0.004$ ).

### Female Choice and Male Competition

Twelve females were successfully mated by nonguarding males, which then adopted the postcopulatory riding position on the female's back. When we introduced a male guarding eggs into the cage, 10 of the 12 females subsequently added eggs to the introduced, guarded brood. Oviposition was preceded by a fight between the two males in all 10 cases where the female added eggs to the existing brood. The fight was initiated by the guarding male, which approached the pair when they passed near



**Figure 1.** Duration (min, log transformed, median and interquartile range) of the precopulatory period, copulation and postcopulatory period for 10 *R. tristis* (□) and 10 *R. carmelita* pairs (■). Differences between the two species were analysed with a Mann–Whitney *U* test: \* $P < 0.05$ .



**Table 1.** Effect of weight on the occurrence and duration of copulation, and pre- and postcopulatory riding

	<i>Rhinocoris tristis</i>		<i>Rhinocoris carmelita</i>	
	Male	Female	Male	Female
<b>Occurrence<sup>†</sup></b>				
Precopulatory riding	0.77	0.63	1.03	-0.54
Copulation	0.81	2.28*	1.51	-0.22
Postcopulatory riding	0.16	3.16*	1.97	-0.89
<b>Duration<sup>‡</sup></b>				
Precopulatory period	-0.45	0.09	-0.02	-0.03
Copulation	-0.60	0.10	-0.52	0.20
Postcopulatory period	-0.19	0.89*	0.16	-0.23

<sup>†</sup>t test with  $df = 97$  for *R. tristis* and 29 for *R. carmelita*.

<sup>‡</sup>Spearman rank correlation,  $N = 10$ .

\* $P < 0.05$ .

the brood. In eight of 10 cases, the guarder 'won' the fight, maintained ownership of the brood and mated with the female before oviposition ( $G_1 = 3.85$ ,  $P = 0.030$ ). In the remaining two cases, the owner 'lost' the fight and the intruder took over ownership of the brood. The females were never seen to attempt to dislodge the riding male on encountering the male guarding eggs. Two of 12 females initiated a brood guarded by the original riding male. In both these cases, the pair did not encounter the guarding male before oviposition.

## DISCUSSION

### Survival, Sex Ratio and Reproductive Rates

Sex differences in survival rates, biased population sex ratios and potential reproductive rates can all affect the direction of sexual selection (Kokko & Monaghan 2001). In assassin bugs, the first two factors did not seem to be important. No sex difference in survival was found in *R. tristis*, nor did we detect any effect of parental care on adult mortality. Even though we could not estimate mortality for *R. carmelita*, we have no reason to expect major differences between these two sympatric species which share similar morphology. In all three locations, the population sex ratio was not biased in either species, suggesting equal investment in the two sexes followed by no sex difference in mortality.

Despite providing parental care, *R. tristis* males had a potentially higher reproductive rate than females: males were observed mating with multiple females at a brood and were seen receiving up to three broods in a single day. In contrast, the maximum rate of egg production by females in the laboratory was one brood per day. This contrasts with male waterbugs, *B. flamineum*, where space on the back of males limits the oviposition rates of females at the beginning of the reproductive season (Kruse 1990). On the other hand, *R. tristis* may be considered analogous with the three-spined stickleback: simultaneous polygyny during care results in a higher male potential reproductive rate despite male investment in parental care (Kynard 1979). Males would therefore be expected to compete for

females and females would be predicted to be the more choosy sex.

*Rhinocoris carmelita* males also had a potentially higher reproductive rate than females: males were able to mate successfully more than once each day and therefore could potentially fertilize two broods each day, whereas a female, even with unlimited food and no need to protect the brood from parasites, could produce only two broods within 18 days. Therefore, like *R. tristis*, *R. carmelita* was expected to conform to the typical sex roles of male competition and female choice.

### Competition and Mate Choice

In accordance with the predictions outlined above, both female choice and male competition were observed in *R. tristis*. First, females preferred males with eggs, although we did not test whether the cue for the preference is the guarding male himself or whether females simply prefer adding eggs to an existing brood. Female preference for guarding males is most likely explained by the higher hatching success of 'added' eggs, compared with first-laid eggs, which is in turn a result of a high likelihood of males abandoning smaller broods, which are subsequently destroyed (Thomas 1994). Broods are probably initiated by females making 'the best of a bad job' when unable to find a suitable existing brood. Second, males were observed competing over females as well as over broods, whereas there was no evidence for competition between females over mates. Male competition for broods can be explained by female preference for males guarding eggs. Unlike most Harpactorinae assassin bugs which lay their eggs on the underside of leaves, *R. tristis* broods are mostly found on plant stems, where they are much more visible. This choice of site may have evolved because of selection on males to expose and advertise their eggs more effectively (Thomas 1994; Tallamy 2000).

The expression of choice is not necessarily restricted to the noncompetitive sex. First, potential reproductive rate theory simply predicts which sex should be the most choosy (Clutton-Brock & Vincent 1991). Second, the expression of mate choice depends not only on potential reproductive rates, but also on variance in mate quality (Owens & Thompson 1994). Female preference for males with eggs (Thomas 1994; L. K. Thomas & A. Manica, unpublished data) suggests that females are the most choosy sex in *R. tristis*. However, there is also a suggestion that males may be discriminating between females: males were more likely to copulate with heavier females and remained with heavier females (which were perhaps more valuable because they were closer to laying) for longer after copulation.

An alternative explanation of the relation between female weight and the likelihood of copulation is that heavier females were more willing to copulate. However, this female-driven interpretation is unlikely for two reasons. First, if heavier females are more likely to mate as a result of female choice, they should also be more willing to accept male advances and engage in precopulatory riding, which was not the case: the mean weight of

females engaging in precopulatory riding was no different from that of females that did not (Table 1). Second, in cases where precopulatory riding took place, but copulation did not, the male dismounted without any aggressive behaviour from the female. Therefore, the relation between female weight and copulation seems best interpreted as a demonstration of male choice. Males seemed to be indiscriminate when first attempting to mate but subsequently discriminated in favour of heavier females, which were likely to oviposit sooner, when copulating and engaging in postcopulatory riding.

*Rhinocoris carmelita* conformed to the typical sex roles. High female investment resulted in a male-biased sex ratio and thus male competition, which was observed under laboratory conditions. Female aggression was short lived and might be better interpreted as predatory behaviour. In contrast to *R. tristis*, the likelihood of copulation did not depend on female weight in *R. carmelita*. The absence of apparent male discrimination between females might be a consequence of low encounter rates with females caused by the low density at which this species occurred in the field. When encounters with females are rare, mate discrimination by males is likely to be too costly. This may result in little effect of female weight on male behaviour, as has been found in studies of other species. For example, male amphipods, *Gammarus lawrencianus*, showed less discrimination between females during precopulatory riding if they had previously spent time in the absence of females (Dunham & Hurshman 1990). Similarly, female encounter rate affected the probability of mate acceptance or rejection in a male zaprochiline katydid (Shelly & Bailey 1992).

### Postcopulatory Riding

Postcopulatory riding was observed in both species of assassin bug, but this behaviour lasted much longer in *R. tristis*, in which all males remained with females after copulation, than in *R. carmelita*, in which males deserted females after mating. Postcopulatory riding has been observed in a large number of insects and is a common feature of reduviid behaviour (Ambrose 1998). The most likely explanation for this behaviour is that a male remains with the female after copulation to prevent her remating with other males and thus reducing the possibility of sperm competition (e.g. Parker 1970; Waage 1979; Sakaluk 1991).

Different population densities in the two species might explain why males were more likely to remain with females after copulation in *R. tristis* than in *R. carmelita*. Yamamura (1986) suggested that postcopulatory riding will be more advantageous at high population densities, owing to the high probability that a female will encounter another male before laying, and *R. tristis* is indeed found at much higher densities than *R. carmelita* (Thomas 1994). A long postcopulatory ride might also have been instrumental in allowing the evolution of paternal care in *R. tristis*, allowing the male to come into contact with the eggs in this internally fertilizing species. Internal fertilization may decrease the likelihood of paternal care

evolving because the male can desert first and leave the female to care for the offspring (Trivers 1972). This contrasts with external fertilization, where the male is last in contact with the eggs and paternal care is relatively common (Trivers 1972; Gross & Sargent 1985). However, the increased likelihood of postcopulatory riding may have occurred after the evolution of paternal care in *R. tristis*: paternal care and competition for egg broods are likely to maintain an extended period of riding as a mechanism ensuring male presence at oviposition.

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