Functional significance of elaborate secondary sexual traits and their evolution in the water strider genus *Rheumatobates*[1]

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Abstract—Sexual conflict may drive the evolutionary elaboration of sexually antagonistic traits that function in mating interactions. One of the most striking cases of elaboration of male morphology occurs in the water strider genus *Rheumatobates* Bergroth (Hemiptera: Gerridae). The functional significance of the bizarre modifications of appendages in this group is not known. Here we focus on one of the more elaborate of the species, *R. rileyi* Bergroth. We conduct observational and experimental studies aimed at determining the general sequence of mating behaviour, the role of females in the outcome of sexual interactions, and the functional significance of the highly modified appendages of males. We also map these traits on a known phylogeny of the genus to determine their pattern of evolution. Males repeatedly harass females and females respond with evasive skating or, if the male successfully grasps her, with a premating struggle. The dynamics of the struggle determine the success of mating attempts. Short struggles typically lead to mating, and long struggles typically result in disengagement of the pair. Following a short period of copulation, males withdraw their genitalia and dismount. Females that have been isolated from males for a period of time become less reluctant to mate. During the premating struggle, the antennae of males are used to grasp the females around the head, and the rear legs are used to lift the females' rear legs off the water surface. Neither antennae nor rear legs are used during copulation, thus they are not used for copulatory courtship. Mapping of these traits on the phylogeny indicates multiple independent origins and a pattern of escalation (16 origins, 7 losses). We conclude that these bizarre traits of males are sexually antagonistic and have evolved repeatedly in the genus.

Résumé—Les conflits sexuels peuvent favoriser le développement au cours de l'évolution de caractères sexuels antagonistes qui servent durant les interactions de l'accouplement. Un des cas les plus remarques de l'élaboration de caractères morphologiques chez le mâle s'observe chez les patineurs du genre *Rheumatobates* Bergroth (Hemiptera : Gerridae). La signification fonctionnelle des modifications bizarres des appendices dans ce groupe reste inconnue. Nous traitons ici principalement d'une des espèces les plus développés à ce titre, *R. rileyi* Bergroth. Des observations et des expériences nous servent à déterminer la séquence générale du comportement d'accouplement, le rôle des femelles dans l'issue des interactions sexuelles et la signification fonctionnelle des appendices fortement modifiés du mâle. Nous plaçons ces caractères sur un arbre phylétique reconnu du genre afin de déterminer leur patron d'évolution. Les mâles harcellent les femelles à répétition et les femelles réagissent en s'éloignant en patinant; cependant, si le mâle réussit à l'attraper, il se produit une échauffourée pré-copulatoire. La dynamique de l'échauffourée détermine le succès de

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la tentative d'accouplement. Les échauffourées courtes mènent normalement à l'accouplement, alors que les échauffourées prolongées se terminent généralement par la séparation du couple. Après une courte période de copulation, le mâle retire ses organes génitaux et débarque de la femelle. Les femelles qui ont été tenues à l'écart des mâles pendant un certain temps sont moins réticentes à l'accouplement. Durant l'échauffourée pré-copulatoire, les antennes des mâles servent à entourer la tête de la femelle et les pattes postérieures sont utilisées pour soulever les pattes postérieures de la femelles au-dessus de la surface de l'eau. Ni les antennes, ni les pattes postérieures ne servent durant la copulation; elles ne sont donc pas impliquées dans la cour associée à l'accouplement. En reliant ces caractéristiques à la phylogénie, on observe de multiples origines indépendantes et un pattern d'escalade (16 origines et 7 pertes). Nous concluons que ces caractères bizarres des mâles sont des caractères sexuels antagonistes et qu'ils sont apparus à plusieurs reprises chez ce genre.

[Traduit par la Rédaction]

Introduction

It is now widely recognized that sexual conflict may occur over a variety of traits shared or influenced by both males and females, including mating rate, oviposition rate, and parental care (Parker 1979; Chapman *et al.* 2003; Arnqvist and Rowe 2005; Rowe and Day 2006). For example, selection on mating frequency may often be opposite in sign in males and females (Parker 1979; Rowe *et al.* 1994; Arnqvist and Nilsson 2000), resulting in sexual conflict over this trait. Such conflicts are expected to lead to the evolution of sexually antagonistic traits in each sex that function to affect the shared trait (*e.g.*, mating rate) in a way that is favourable to its bearer. Examples of sexually antagonistic morphological traits that have evolved in this context include various grasping structures in males (Wing *et al.* 1983; Thornhill 1984; Arnqvist 1989; Sakaluk *et al.* 1995) and at least one counter adaptation in females (Arnqvist and Rowe 1995). In one genus of water strider (*Gerris* Fabr.), sexually antagonistic traits of males and females have been shown to coevolve (Arnqvist and Rowe 2002).

The mating system of many water strider species (Heteroptera: Gerridae) is often characterized by intense sexual conflict over mating decisions including mating rate (Rowe *et al.* 1994; Arnqvist 1997). Females store sperm, with the result that mating is often superfluous for females, and mating entails a variety of costs to females (Rowe *et al.* 1994; Arnqvist 1997). Conflict over mating rate is manifest as a high rate of mating attempts by males, and female resistance to these attempts in the form of dramatic premating struggles during which females struggle vigorously in an attempt to dislodge persistent males (*e.g.*, Arnqvist 1992; Rowe 1992; Weigensberg and Fairbairn 1994; Vepsäläinen and Savolainen 1995). Resistance of females is modulated by the costs of mating itself and the costs of resisting males (Rowe 1992, 1994), and has been referred to as convenience polyandry (Rowe 1992). Female resistance in turn favours the elaboration of sexually antagonistic grasping in males (reviews in Arnqvist 1992, 1997; Rowe 1994; Rowe *et al.* 1994). For example, in *Gerris odontogaster* (Arnqvist, 1989), males possess a pair of abdominal spines that enhance the male's ability to withstand premating struggles and are thus favoured by female resistance. Males within several other water strider genera possess a variety of elaborate structural features, which may likewise serve as grasping devices during mating (Andersen 1982; Arnqvist 1997).

Rheumatobates Bergroth is a New World genus of small water striders that belong in the subfamily Rhagadotarsinae (Andersen 1982). Hungerford (1954) described this genus as one of the most remarkably modified groups within the Hemiptera. Some of the most extreme modifications of male appendages occur in *R. rileyi* Bergroth, 1892 (Hungerford 1954). Elaborated male characters include antennae that are thickened, twisted, and provided with bizarre outgrowths, and rear legs that have a peculiar twist of the femora, an attachment of the rear tibia apart from the apical end of the femur, and a dense cluster of hairs on the rear femur and tibia (Silvey 1931) (see Fig. 1). These modifications appear to slow development in males and may increase mortality rate (Westlake and Rowe 1999). Previous studies of *R. rileyi* suggest that these structures function as adaptations for grasping females during copulation (Silvey 1931). Males supposedly use their antennae and rear legs to grasp females anteriorly and posteriorly, respectively. This raises the possibility that these structures stimulate females during copulation and are favoured by cryptic female choice (Eberhard 1985, 1996). Alternatively, these structures may be sexually antagonistic traits used to grasp females during premating struggles. No detailed study of mating or the function of these structures has been undertaken.

Sexual conflict is viewed as a key force driving the exaggeration and diversification of behaviours and secondary sexual structures that are sexually antagonistic (*e.g.*, Parker 1979; Holland and Rice 1998; Gavrilets *et al.* 2001; Rowe *et al.* 2005). However, there have been very few evolutionary studies of the diversification of sexually antagonistic traits (Bergsten *et al.* 2001; Arnqvist and Rowe 2002; Koene and Schulenburg 2005). In the case of the bizarre modifications of the appendages of male *Rheumatobates*, we have little evidence that the structures are sexually antagonistic, and their evolution has not been studied. In the absence of a phylogeny, Andersen (1982) postulated that the evolution of these traits was relatively conservative. In contrast, in their phylogenetic treatment of the genus, Westlake *et al.* (2000) discovered a great deal of diversity within traits, raising the possibility that there has been repeated and divergent evolution of the various structures. The presence of a phylogeny now allows this question to be resolved.

The aims of this paper are to (*i*) describe the mating behaviour of *R. rileyi*, (*ii*) determine the role of female resistance in the success of premating struggles in *R. rileyi*, (*iii*) determine the functional significance of modified male appendages in *R. rileyi*, and (*iv*) trace the evolution of these appendages on the phylogeny of *Rheumatobates*.

Methods

Collections

For the behavioural work, multiple field collections of live *R. rileyi* were made during July and August from a pond on Lot 16, Concession 10, Manvers Twp. near Bethany, Ontario, Canada. Bugs were transported back to the laboratory. All data were collected from observations of adult bugs.

Behavioural observations

In preliminary experiments and those described below, we observed adults in the laboratory for more than 100 h. All laboratory observations and experiments were conducted on mixed-sex cultures of one to several pairs in plastic pools (0.25 m^2) under artificial light (16L:8D). We also observed adults in the wild for approximately 40 h at the field collection site and at Smoke Lake in Algonquin Park, Ontario. These laboratory and field observations formed the basis of our description of the mating sequence of *R. rileyi* and the function of elaborated male appendages. During observations, we recorded the presence and absence of pre- and post-mating struggles, copulation, postcopulatory guarding, and the use of antennae and fore, mid, and rear legs by males.

Mating duration

In the first experiment, we determined the mean mating duration of 28 females. Bugs were held in single-sex cultures at densities of <50/m^2 for 24 to 48 h prior to mating trials. Therefore, mating had not occurred for at least 24 h. At the beginning of the trial, one female and four males were placed in the observation pool. In this experiment, the first struggle always led to copulation. We timed the duration of the struggle and the duration of mating with a handheld stopwatch. Because we had relatively few males, males that had not yet mated were used again up to three times. Females were never reused.

Postmating resistance in females and durations of successful and unsuccessful struggles

Previous studies of the water striders *Gerris* spp. and *Aquarius* spp. (*e.g.*, Rowe 1992; Weigensberg and Fairbairn 1994; Lauer 1996) have shown that the duration of premating struggles reflects female resistance to mate: those struggles that lead to mating ("successful struggles") are typically shorter than those that do not ("unsuccessful struggles"). To determine the durations of successful and unsuccessful mating attempts, we first isolated 10 females for 24–48 h, then exposed them separately to four males until mating had occurred, and then immediately exposed them to a new set of four males. Our expectation was that females would be most resistant to mating attempts immediately after mating. Because females were exposed to new males in the second exposure, any change in mating behaviour between the first and second exposures can be attributed to the effect of prior mating on females rather than on males.

In both exposures to males, we recorded premating struggle duration, the outcome of the struggle, and copulation duration if the struggle was successful. Struggles began when males grasped females and ended when females escaped or copulated. In the first exposure, trials were terminated after copulation, and in the second exposure, after copulation or after three struggles of greater than 4 s duration had occurred. We used a 4 s cutoff because our preliminary studies indicated that successful struggles were typically 3 s or less.

Immobilization of the antennae

To determine the functional utility of male antennae for grasping females, we immobilized male antennae by gluing them together with Crazy Glue®. This manipulation kept antennae in their typical tip-down position but held them together so that they could not grasp females. Males and females were isolated for 24 h prior to the experiment, in same-sex pools with abundant food. At the beginning of the experiment, males were anesthetized with CO_2 and antennae were glued. Control males were also anesthetized but their antennae were not glued. After this procedure, glued and control males were returned to their holding tanks and allowed to feed for 3 h. The experiment began following this feeding period, when each male was placed in a pool with a female and behaviour was observed. Seventeen glued males and 17 control males were tested alternately over 2 days. We recorded the number of mating attempts, which could be divided into three types: (1) harassment events, where males lunged at females but did not grapple the females; (2) partial premating struggles, where males grappled the females but did not gain the mating position and the females responded by struggling; and (3) struggles, where males grasped the females in the mating position and females responded by struggling. We also measured the time to mating. Each trial lasted 20 min or until mating occurred.

Trait mapping

We traced the evolution of the four male appendages that are modified in males and that may act as grasping structures (antennae, fore legs, mid legs, and rear legs) (Fig. 1) onto the existing phylogeny of *Rheumatobates* (Westlake *et al.* 2000). Westlake *et al.* (2000) and Westlake (1998) provide detailed descriptions of the focal characters of this study. There is great diversity among species in the details of modification of each appendage; thus, the “modified” state of any particular appendage breaks down into a number of specific states (“kinds” of modified trait), each of which defines a different kind of morphological modification of a particular male trait. For the purpose of mapping, modification of any one appendage was scored as the same “kind” of modified trait if at least one distinct modification was shared and we were confident that the shared modification was homologous. In most cases, modified traits that were defined as the same kind (homologous) shared more than one distinct modification. The character states were extracted from Westlake *et al.* (2000), and further discussion of the data set and mapping exercise is given in Westlake (1998). Character optimization onto the preferred tree of Westlake *et al.* (2000) was conducted using ACCTRAN optimization within MacClade 3.0 (Maddison and Maddison 1992).

Results

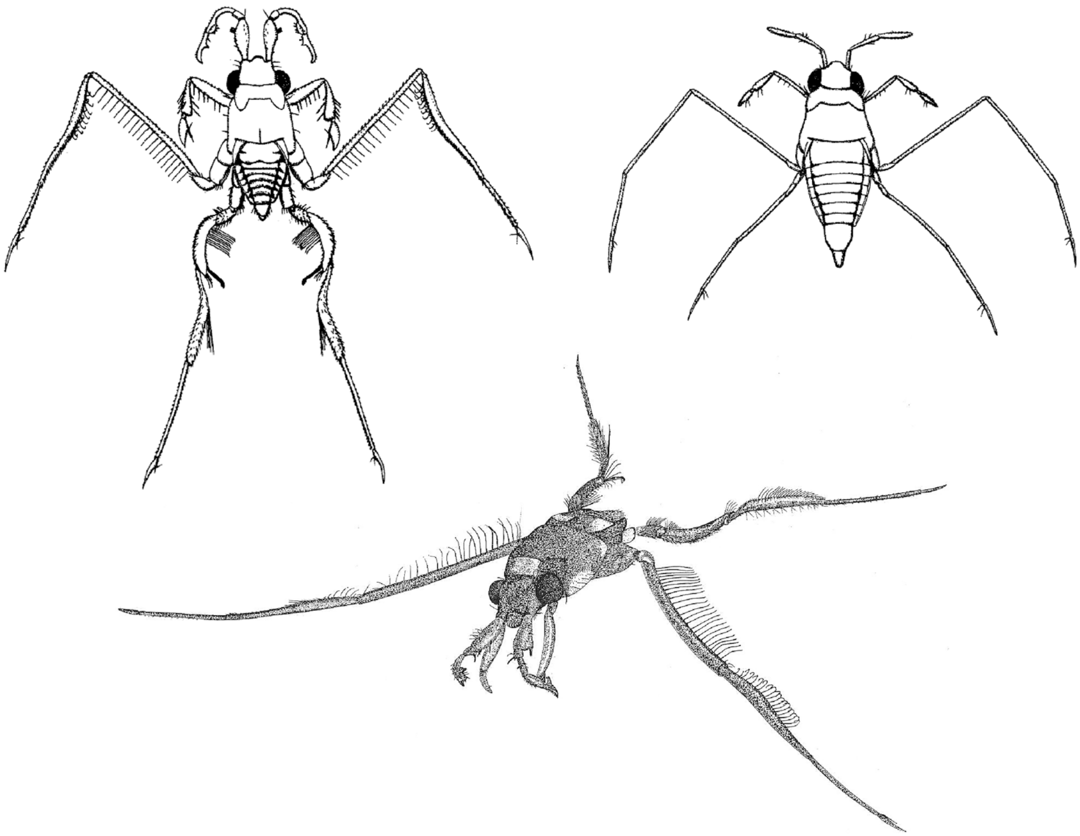
Mating behaviour

There are four components to the mating behaviour of *R. rileyi*: mating attempts, premating struggles, copulation, and termination of copulation. There is no postmating guarding or struggling at the termination of mating.

Males initiate contact with females by simply lunging at females without prior courtship. Females attempt to avoid males in numerous ways. They skate and jump away or, on occasion, aggressively lunge at harassing males. Males are indiscriminate in their efforts, often lunging at conspecific males. Either the male fails to make firm contact with the female and she escapes or the male grasps the female and a premating struggle ensues.

Females are generally reluctant to mate and attempt to dislodge the male by leaping, rocking, and somersaulting. In only a few instances was a male observed mounting a female without such a premating struggle. The following describes the behavioural components that appear to be relatively invariable in the premating struggle (although their order within the struggle sequence is variable). A male that successfully achieves physical contact with a female grasps the female’s thorax with his fore legs. He attempts to grasp the female’s head with his barbed antennae

Fig. 1. Dorsal views of male (top left) and female (top right) adult *Rheumatobates rileyi* and a lateral view of the male (bottom).



and (or) snatch up the female's rear legs with his modified rear legs. These manoeuvers render the female relatively immobile. On occasion the male appeared to use his mid legs similarly on the female's mid legs.

Struggles were so brief that it was necessary to decide *a priori* to note either the function of the antennae or the function of the rear legs during observations. Given this constraint, it was difficult to establish the typical order and frequency of manoeuvers during struggles. Males were repeatedly observed squeezing their rear legs together when a struggle was initiated and were often successful in clasping the female's rear legs in this manner. This was taken as a reasonable indicator that males were trying to grasp females with their rear legs. Males that used their rear legs in this manner did so immediately upon contact with a female. During the initial stages of several struggles, the female's rear legs were actually seen tangled up in the hairs covering the bowed femurs of the male's modified rear legs. In cases where details were clearly observable, males subsequently grasped at the female's head with their antennae. Males do not attempt to insert genitalia during the struggle but rather concentrate efforts on subduing the female with their modified appendages.

Copulation starts if the pair ceases struggling and the male successfully inserts his genitalia. A calm pause precedes copulation. In a few instances, males willingly dismounted at this stage without any attempt at intromission. The pause ends when males twist their rear legs at a 45° angle to their body, which is associated with insertion of the genitalia. The pair is typically active (*e.g.*, skating and jumping) for about 15–30 s directly after insertion, after which time activity is minimal until mating ends. Once copulation commences, males cautiously release their antennal grip (one by one) but maintain their fore-leg grasp of the female's thorax. At no time during the copulatory phase do males use their modified antennae or rear legs as either courtship or grasping apparatus. Attempts by second males to disrupt pairs elicited little response from pairs and never resulted in takeover or interruption.

The male terminates all copulations without a struggle. After withdrawing his genitalia, the male simply dismounts the female. There is no postcopulatory contact or non-contact guarding. An increase in activity by the female (*e.g.*, skating and jumping) is associated with the last 30 s of mating. During termination, the male typically opens and untwists his rear legs (indicating withdrawal of genitalia), arches his body off the female, and dismounts. The female's sword-like ovipositor is emitted simultaneously and retracted again almost immediately.

Mating duration

Of the 28 females that we exposed to males, all mated after the first struggle. The mean struggle duration was quite short (2.68 s, SE = 0.11). The mean mating duration was 283.36 s (SE = 6.71).

Postmating resistance and durations of successful and unsuccessful struggles

In the first exposure to males, 9 of 10 females mated after the first struggle with a male. One female mated after three struggles. In the subsequent exposure to males, all 10 females resisted further matings (see Methods). To compare the durations of successful and unsuccessful struggles, we used a paired *t* test. Each of the 10 females had one successful struggle in the first exposure and three or more unsuccessful struggles in the second exposure (mean = 8.4). The mean duration of successful struggles was 3.71 s (SE = 0.27, n = 10) and the mean duration of unsuccessful struggles was 7.29 s (SE = 0.463, n = 10). Successful struggles were significantly shorter than unsuccessful struggles (paired *t* test; $t_9 = -6.92$, $P < 0.0001$). The average rate (no./min) of harassment per unmated female was 0.36 (SE = 0.01) in the first exposure and 0.35 (SE = 0.01) in the second exposure. The mean mating duration of these 10 females was 272.55 s (SE = 12.24). As in the prior experiments, there was no guarding period and no postmating struggle.

Immobilization of the antennae

Males were unable to mate when their antennae were immobilized. Of 17 males tested, none achieved a mating in the 20 min experiment, whereas all control males mated. The lack of mating by glued males was not because of a lack of mating attempts. Glued males attempted to mate at a rate of 4.7 times/min (SE = 1.2), whereas control males attempted to mate at a rate of 1.7 times/min (SE = 0.3). The rates in the glued group were significantly higher than those in the control group (ANOVA; $F_{1,32} = 5.3$, $P = 0.02$). We suspect that the higher rate of mating attempts among glued males resulted from increased rates of attempts over the 20 min period, and most control males mated very early in this period. The mean time to mating was 2.9 min (SE = 0.7) in the control group. Glued males frequently attained a partial grasp of females, averaging 1.9 (SE = 1.2) partial struggles/min, but were never able to gain the mating position, and females escaped the males in every case.

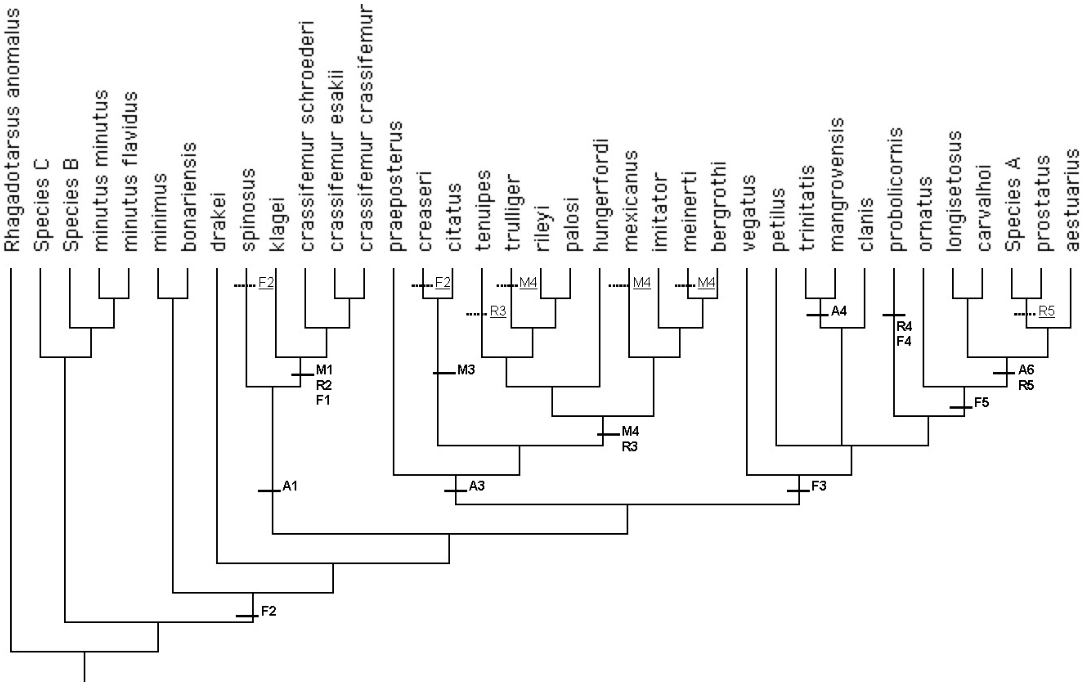
Mapping of traits

Optimization of the four male traits onto the phylogeny illustrates that there have been multiple independent origins of modifications of each trait (Fig. 2). Therefore, there are multiple "kinds" of each modified trait, resulting from multiple evolutionary transitions. More specifically, in antennae there were four transitions to distinct states and no transitions back to the pleisiomorphic state, in fore legs there were five transitions to distinct states and two transitions back to the pleisiomorphic state, in mid legs there were three transitions to distinct states and three transitions back to the pleisiomorphic state, and in rear legs there were four transitions to distinct states and two transitions back to the pleisiomorphic state. Moreover, of the 16 origins of distinct states, losses back to the pleisiomorphic state occurred within only 4 of these. This biased pattern toward origins suggests a pattern of escalation of these male traits.

Discussion

Our studies suggest that the mating system of *R. rileyi* shares many features with the systems of the better known water strider genera *Gerris* and *Aquarius* (Schellenberg) (Rowe *et al.* 1994; Arnqvist 1997). Like males of these other genera, male *R. rileyi* are persistent in mating attempts, and females are resistant, leading to dramatic premating struggles. The degree of female resistance modulates the success of male mating attempts and, as would be predicted, the bizarre modifications of male appendages appear to function in overcoming this resistance. Tracing the evolution of these traits on the phylogeny suggests that there have been multiple

Fig. 2. The preferred phylogeny of the genus *Rheumatobates* (from Westlake *et al.* 2000) with the transitions between elaborated and non-elaborated appendage states mapped on. These include antennae (A), fore legs (F), mid legs (M), and rear legs (R). Transitions forward from non-elaborated to elaborated are marked with a solid line and are boldfaced. Transitions back to the pleisiomorpic state are marked with a dotted line and are underlined. The numbers beside each transition refer to distinct elaborations of a given trait (see text, Westlake 1998, and Westlake *et al.* 2000).



independent origins of elaborated appendages and that there is a trend toward escalation (Fig. 2).

Mating behaviour

Numerous previous studies of the economics of mating in *Gerris* and *Aquarius* water striders have shown that there is sexual conflict over mating rate (reviews in Rowe *et al.* 1994; Andersen 1997; Arnqvist 1997). This conflict is manifested in the conspicuous premating struggles of many gerrids, which modulate the rate of mating. Although we have not conducted these sorts of economic studies on *R. rileyi*, the mating behaviour suggests similar sexual conflict in this species. Several prior studies of *Gerris* and *Aquarius* spp. have demonstrated that females play a preeminent role in determining the outcome of premating struggles. There is good evidence that females balance the costs of mating against those of a long struggle, which is often required to dislodge males (*e.g.*, Arnqvist 1992; Rowe 1992; Weigensberg and Fairbairn 1994; Vepsäläinen and Savolainen 1995). Shorter struggles are typically associated with mating, whereas longer struggles lead to the dislodging of the male. The current study of *R. rileyi* supports this view: struggles that led to mating were, on average, significantly shorter than those that did not. These data suggest that successful mating attempts, to a large degree, result from a lack of female resistance rather than greater male persistence, as has been shown in *Gerris* spp. (Arnqvist 1992; Rowe 1992). If females do not want to mate, premating struggles, once initiated, continue until the male is dislodged. Likewise, in the current study, when female *R. rileyi* resistance was low (first exposure to males), mating rate was very high, whereas when female resistance was high (second exposure to males), mating rate was very low.

It is not clear why female resistance increased greatly following copulation. Previous studies have shown that female *Aquarius remigis* (Say, 1832) and *Gerris buenoi* Kirkaldy, 1911 have greatly reduced resistance to male mating attempts when they are virgins or when they have run out of sperm (Lauer 1996; Ortigosa and

Rowe 2003). It is certainly a possibility that females in the first exposure to males (in this experiment) were depleted of sperm, whereas those in the second exposure were not because they had just mated. However, just 24–48 h prior to the experiment, females had been held in cultures with males, and therefore it seems highly unlikely that they had not mated very recently. Sperm storage in those water strider species that have been studied is typically greater than 10 days, though it has not yet been studied in *Rheumatobates* spp.

There are other elements of the behaviour of *R. rileyi* that differ from the behaviour observed in past studies of *Gerris* and *Aquarius* water striders. First, there appears to be no guarding period following copulation, as there is in *Gerris* spp. (Rowe *et al.* 1994; Andersen 1997; Arnqvist 1997). We saw no evidence of guarding in *R. rileyi*: after a short copulation period (~4–5 min), males withdrew their genitalia and dismounted the females. In *Gerris* spp., males switch from copulation to guarding by withdrawing their genitalia but continuing to stay mounted on the females (Arnqvist 1992; Rowe 1992). This guarding period, which can last much longer than the copulation, ends with a vigorous struggle intiated by females, a behaviour that was also absent in *R. rileyi*. In *Aquarius* spp., there is also no distinct guarding phase, but copulation can last hours and often ends with a struggle initiated by females (Weigensberg and Fairbairn 1994).

The function and evolution of sexually antagonistic traits in males

Earlier studies of *Gerris* spp. demonstrated that female resistance favours the elaboration of antagonistic grasping traits in males (Arnqvist 1989; Ortigosa and Rowe 2002). Our data support the hypothesis that the modified appendages of male *R. rileyi* are sexually antagonistic traits, whose function is to overcome female resistance. The antennae, fore legs, rear legs, and possibly mid legs are employed in grasping the female during premating stuggles. In a previous study, Silvey (1931) noted that the male antennae were used during copulation to grasp the female firmly anteriorly while the rear legs were curved around those of the female, thus providing posterior attachment. Silvey (1931) concluded that these modified appendages were adaptations for copulation. Recent interpretations might suggest that they function in copulatory courtship and could be favoured by cryptic female choice (Eberhard 1985, 1996). Our observations suggest that males release the grasp of both the antennae and the rear legs as soon as the female stops struggling. Thus, these grasping structures do not aid in keeping the sexes together during mating but serve in gaining a purchase on females during premating struggles. Moreover, because these structures are not employed during copulation, they do not function as copulatory courtship devices.

Presumably, these structures effectively decrease the opportunity to escape and (or) increase the cost of struggling for the female (*e.g.*, energy expenditure and costs of injury). The inability of males with immobilized antennae to achieve any mating, despite repeated attempts, suggests that these appendages, at least, are also required for males to overcome female premating struggles. Future manipulation of the other appendages may confirm that they too are required in overcoming female resistance. Nevertheless, our data suggest that sexual conflict over mating frequency leads to female resistance, and resistance in turn has led to the evolution of sexually antagonistic grasping appendages in males.

Earlier detailed morphological study of the modified appendages of male *Rheumatobates* suggested that there was a great structural variety in the modification of each appendage (Westlake *et al.* 2000). Using these data, combined with a phylogeny, we have shown that modification of each of the male appendages has happened multiple times to create this diversity (Fig. 2). Combined with our behavioural observations, these data suggest that sexual conflict has led to a great diversity of sexually antagonistic traits in male *Rheumatobates*. A conservative estimate suggests that there have been 16 independent modifications of these appendages and 7 transitions back to the pleisiomorphic state (Fig. 2). The bias toward forward transitions results in a pattern of escalation, where modifications of the appendages are added one upon the other during evolution. This pattern of escalation is predicted in some theories of sexually antagonistic coevolution and is reflected in the common phrase "arms race" (Holland and Rice 1998; Gavrilets *et al.* 2001; Rowe *et al.* 2005). However, an earlier study of sexually antagonistic coevolution in *Gerris* spp. suggests a much more bidirectional pattern, in which there are periods of both escalation and retreat (Arnqvist and Rowe 2002).

It is interesting to note that no corresponding sexually antagonistic structures appear to have evolved in female *Rheumatobates*. Westlake (1998) and Westlake *et al.* (2000) could find no obvious anti-grasping traits in females. In *Gerris* spp., such traits in females have been found and have been demonstrated to be coevolving with male grasping traits (Arnqvist and Rowe 1995, 2002). Perhaps female behaviours, rather than morphology, have evolved in response to the evolution of antagonistic male morphology in *Rheumatobates* spp. An answer to this question will require detailed comparative study of female behaviour in species that have coevolved with males that are unmodified and those that are modified.

Conclusions

As in many other water striders, the mating system of *R. rileyi* appears to be characterized by intense sexual conflict over the decision to mate. Male mating success varies as a direct consequence of variation in female resistance to mating. In response to this general resistance, males have evolved various structural adaptations that aid in grasping females efficiently during precopulatory struggles. There is a great diversity of these antagonistic traits within the genus *Rheumatobates* (Westlake *et al.* 2000), and our analyses suggest that these distinct modifications of each appendage have evolved multiple times independently.

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