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The costs of mating and mate choice in water striders

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Abstract. Predation risk associated with the various components of the mating behaviour of the water strider *Gerris buenoi* are investigated with a series of experiments. Mating behaviour in this species includes frequent harassment of females by males (mate searching), pre-mating struggles that may function as mate choice by females, mating which includes copulation and male mate guarding, and post-mating struggles. Each component of the mating behaviour of females increases predation risk. Escape by females from harassment by males increases the movement rate of females and predacious backswimmers are attracted to movement at the water surface. Capture success of backswimmers is almost tripled on females engaged in pre- and post-mating struggles relative to single females. Because longer pre-mating struggles are one mechanism by which females bias the mating success of male phenotypes in water striders, these data demonstrate that mate choice is costly to females. Finally, mating females are at twice the risk of predation than are single females. Some components of mating behaviour in males also appear to increase predation risk. Males searching for mates spend a higher portion of their time in the open water habitat (out of refuge) and move more often than females. Use of the open water habitat increases exposure to backswimmers and movement on the surface attracts backswimmers. Males that successfully grasp females engage in pre-mating struggles, during which capture success by backswimmers on males is significantly increased. However, in contrast to females, there was no significant increase in capture success of backswimmers on mating relative to single males.

It is a commonly held view that mating involves costs to both sexes (Daly 1978; Walker 1980; Gwynne 1989). Males should be more willing to pay costs than females, because mating frequency is more likely to directly limit reproductive success in males than females. Indeed, recent reviews suggest that mating costs, particularly predation risk, are more prevalent in males than females (Gwynne 1989; Magnhagen 1991). Yet, elevated predation risk to females may play an important role in structuring mating systems, although evidence so far is scarce (Gwynne 1989; Magnhagen 1991).

Distinguishing the components of mating behaviour that are costly to females is informative for the evolution of life histories, mating systems and secondary sexual traits (e.g. Partridge & Endler 1987; West-Eberhard 1987; Pomiankowski 1988; Crowley et al. 1991; Curtsinger 1991; Kirkpatrick & Ryan 1991). For example, the behaviour patterns used in mate choice may increase predation risk and a cost to mate choice is critical in distinguishing among models of sexual selection (Pomiankowski 1988; Kirkpatrick & Ryan 1991). Multiple mating may be favoured if sexual harassment of females by males imposes a cost to females (Convenience Polyandry, sensu Thornhill & Alcock 1983; Rowe 1992a). Alternatively, copulation itself may increase risk to females and such a cost will tend to favour reduced mating frequency by females.

Several recent studies have suggested a role for predation risk in the ecology and evolution of water strider mating behaviour. Female *Gerris buenoi* Kirkaldy retreat to refuge when mating commences (Rowe 1992a), mating activity of *Aquarius remigis* is reduced in the presence of predacious fish (Sih et al. 1990) and two studies present evidence of increased predation risk to females when mating (Arnqvist 1989a; Fairbairn 1993). As part of an economic analysis of the mating system of *G. odontogaster*, Arnqvist (1989a) demonstrated that predation by

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backswimmers (Heteroptera: Notonectidae) on females in the laboratory increased in the presence of males. Fairbairn (1993) found that predation by frogs on copulating pairs of *A. remigis* was higher than on single gerrids. Arnqvist's study does not, however, address how the presence of males increases risk to females. Fairbairn's study focuses on copulation, but is so far the only study to demonstrate an increased risk of predation to copulating females of any species.

Non-random mating success of males appears to be common to water striders including *G. buenoi* (Fairbairn 1988; Arnqvist 1989b, 1992a, b; Sih & Krupa 1992; unpublished data). Mating is preceded by a struggle initiated by the female. Short struggles usually result in mating while longer struggles do not (Arnqvist 1992c; Rowe 1992a). Females may either bias the duration of struggles toward certain male phenotypes (e.g. large size, large mate clasping apparatus) and/or those same phenotypes may simply be better able to withstand longer struggles. There is as yet no evidence of the former mechanism, however, there is direct evidence for the latter in a species closely related to *G. buenoi* (Arnqvist 1989b) and supportive evidence in another species (Sih & Krupa 1992). In either case, the struggle is the behavioural mechanism by which females bias mating success of males toward certain phenotypes, and is thus by definition the mechanism of mate choice (Maynard Smith 1987; Pomiankowski 1988).

The magnitude of female reluctance to mate (struggle duration) varies with both the rate of male harassment of females and the costs of mating to females (Rowe 1992a). Given that reluctance is the mechanism of mate choice, the degree of non-random mating is predicted to vary inversely with female reluctance (Arnqvist 1992a, b). Indeed, this model of mate choice successfully predicts variation in non-random mating success of males in both the laboratory and the wild (Arnqvist 1992a, b; Sih & Krupa 1992). However, non-random mating success of males may come at a cost to females. Pre-mating struggles may attract predators and result in increased vulnerability. If so, then mate choice by females is costly. To my knowledge there is no direct evidence that mate choice behaviour patterns increase predation risk to females of any species.

In the present study I assess the predation risk associated with each component of the mating behaviour of male and female *G. buenoi*. I focus on risk imposed by predacious backswimmers on each component of mating behaviour: harassment of females by males, pre- and post-mating struggles (the means of mate choice), and mating (copulation/guarding). I focus on predation by backswimmers because they are known to be a major predator of larval and adult gerrids in the wild (Spence 1983, 1986; Rowe 1992b). Mortality rates of adult *G. buenoi* resulting from back swimmer predation are typically female biased in field enclosures (Rowe 1992b) and Arnqvist's (1989a) laboratory experiment on *G. odontogaster* suggests that this bias is the result of mating behaviour (see above).

METHODS

Gerris buenoi is a small partially bivoltive gerrid, common to both temporary and permanent habitats throughout much of North America (Spence & Scudder 1980). In the experiments reported here, I used macropterous overwintered bugs. These adults emerge from diapause in the early spring to mate and reproduce for the remainder of their adult life (a few weeks to months). Females mate freqently and oviposit approximately daily during this period (Rowe & Scudder 1990; Rowe 1992a). The mating system of *G. buenoi* has been described (Rowe 1992a). Males make frequent attempts to mate with females (harassment) and females respond by initiating vigorous pre-mating struggles. Most struggles occur on the open water and few end in copulation. Males ride on the backs of females during copulation and subsequently during guarding of the females. I will refer to the combination of copulation and guarding periods as the mating period. Mating is terminated by a struggle initiated by females.

Habitat Use and Activity Level

Both male and female *G. buenoi* spend a significant time on top of floating debris (grooming, feeding, resting, etc.; Rowe 1992a) that serves as a refuge from predation by backswimmers (which attack from below). Sexes may vary in the use of refuge because of their sexual behaviour and thus in the duration of time that they are exposed to predatory attacks by backswimmers. To determine whether use of refuge varied between the sexes, I documented the proportion of observed individuals of each sex that occurred on either open water or floating debris (refuge). Three surveys, at Shallow Pond in the University of British Columbia Botanical Gardens (see description in Rowe 1992a), on 27, 29 June and 1 July, were conducted from the shore with a pair of binoculars. On each date, I surveyed the same patch of pond surface (approximately 1 × 3 m) that contained a dense concentration of single and mating gerrids. Foraging backswimmers were common throughout this small pond.

Backswimmers are attracted to movement on the water surface and are even able to discriminate movements of prey (including skating gerrids) from non-prey items (Lang 1980). Thus, movement of gerrids on the water surface is expected to increase attack rates. I, therefore, compared the movement rates of males and females in the laboratory when held with their own sex or with the opposite sex, to determine whether the sexes differ in their movement rate and if sexual behaviour independently increases movement rate.

Gerrids used in these laboratory experiments were collected from Shallow Pond and held for 24–48 h prior to the experiment in large plastic wading pools (separated by sex) in the laboratory with abundant food (fruit flies). For the experiment, I placed six marked individuals in a single experimental pool for a 15-min acclimatization period followed by a 10-min period of observation. Experimental pools were constructed of Plexiglas and had a surface area 0·5 m^2 and depth of 3 cm. I chose an individual at random and counted the number of movements (strides) made over the 10-min period. Occasionally, focal individuals would skate into a corner and repeatedly run into the Plexiglas. When this disturbing behaviour occurred, I switched to a new focal individual. I compared three treatments: (1) six females (five replicates), (2) six males (five replicates) and (3) three males+three females (10 replicates). Replication of the latter treatment was doubled because in any replicate I followed either a male or female. Therefore, the experiment included five replicates each of a focal male among males, female among females, male among both sexes and female among both sexes. Treatments were alternated over a 2-day period.

Backswimmer Capture Success

To determine whether mating and struggling bugs are at greater risk of predation, I compared the capture success of backswimmers on single males and females, and males and females engaged in struggles (pre- or post-mating) and mating (copulation or guarding). Pre- and post-mating struggles include the same behaviour patterns, although post-mating struggles are somewhat longer (Rowe 1992a). I was unable to distinguish them during this test, therefore I have lumped them together for analysis. Nevertheless, most of the struggles observed here were probably pre-mating struggles because mating was relatively rare.

This experiment was conducted in the laboratory pools with gerrids collected and maintained as in the previous experiment. I placed 10 males and five females, marked according to sex, in pools containing four adult *Notonecta kirkii.* I used a 2:1 sex ratio to increase the number of observable inter-sexual interactions. Backswimmers were starved for 24–48 h prior to the experiment. Over a 1-h period, I recorded all attacks by backswimmers on single males and females, mating or guarding pairs, and pairs engaged in pre- or post-mating struggles. Captured gerrids were removed and replaced as soon as the success of the attack was determined. The experiment was repeated four times over a 2-day period, with new gerrids and backswimmers in each replicate. I defined (1) attack, as a lunge towards and attempt to grasp a gerrid or gerrids, (2) capture, as those attacks by backswimmers that resulted in the gerrid or gerrids being pulled under water, (3) capture success, as the ratio of captures to attacks and (4) predation, as an immobilization of the captured gerrid.

RESULTS

Habitat Use and Activity Level

On all three survey dates a higher proportion of females than males were found on the refuge of floating vegetation. The proportion of individuals on floating vegetation was 0·68 (N=40), 0·73 (N=55) and 0·81 (N=37) for females and 0·47 (N=36), 0·32 (N=47) and 0·46 (N=37) for males. The pooled chi-squared (30·23) indicated a significant difference (P<0·001) in habitat use (paired

Table I. The effect of sex and presence of the opposite sex on stride rate

	Single-sex groups		Mixed-sex groups	
	Male	Female	Male	Female
$\bar{X}$ Stride rate	126·8	85·2	137·6	106·8
SE	7·4	3·7	6·9	8·3

$N=5$ for each group.

Table II. The effect of state activity of gerrids (single, mating, wrestling) on the mean (±SE) number of attacks and mean (±SE) proportion of captures by backswimmers

	Single	Mating	Wrestling
Number of attacks (male/female)	47·0 ± 1·8/22·0 ± 2·7	10·0 ± 1·9	5·5 ± 1·3
% Capture (total)*	10·4 ± 1·3	29·7 ± 4·7†	49·8 ± 6·7†
% Capture (male)*	10·5 ± 1·7	3·8 ± 2·3	21·5 ± 2·3†
% Capture (female)*	10·2 ± 1·0	25·8 ± 5·9†	28·3 ± 2·8†

$N=4$ for each category of behaviour.

*Indicates overall significant effect of state (ANOVA).

†Indicates a significant difference between the adjacent mean and the value for single gerrids in that row.

t-test comparing proportions on the three dates similarly indicated a significant difference, $P<0{\cdot}05$). In independent surveys of this pond (1992a), I found that 89% of 276 mating females were found on refuge. This figure is significantly greater than the mean proportion on single females found on refuge in the current surveys ($\chi^2=15{\cdot}17$, $P<0{\cdot}001$). Thus females appear to use refuge more often when mating than when single as suggested by earlier behavioural observations (Rowe 1992a).

In the laboratory experiment males moved more frequently than females when grouped with their own sex or the opposite sex and the presence of males increased the movement rate of females (Table I). Movement rate of individual gerrids was significantly affected by both sex and grouping, and there was no significant interaction between the factors (ANOVA: sex: $F_1=28{\cdot}4$, $P<0{\cdot}001$; group: $F_1=5{\cdot}7$, $P=0{\cdot}03$; sex × group: $F_1=0{\cdot}6$, $P=0{\cdot}439$). Males actively harassed (chased and attempted to mount) both males and females during these experiments. Females rarely chased other females or males, but frequent harassment by males resulted in a 25% increase in movement rate of females grouped with males compared with those grouped with other females.

Backswimmer Capture Success

Capture success of backswimmers was higher on mating and wrestling pairs than on single gerrids, and females were more likely to be preyed upon than males when backswimmers captured pairs (Table II). No significant difference in capture success of backswimmers was detected between attacks on single males and females. Therefore, I first analysed the effect of state (single, mating or struggling) on capture success independently of which sex was captured (Table II) and then repeated it for each sex. Individual means are then compared with a Tukey test.

There was a significant effect of state on total capture success (ANOVA, $F_2=28{\cdot}8$, $P<0{\cdot}001$). Backswimmers were about three times more successful in attacks on mating pairs than on single gerrids and about five times more successful in attacks on wrestling pairs than on singles. These two values were significantly different from the mean capture success on single gerrids ($P<0{\cdot}02$ and $P<0{\cdot}001$, respectively). There was a significant effect of state on capture success of females (ANOVA, $F_2=13{\cdot}6$, $P<0{\cdot}002$). Females were captured in 25·8% of attacks on mating pairs, and in 28·3% of attacks on struggling pairs. These two values were significantly different from the mean capture success on single females ($P<0{\cdot}005$, $P<0{\cdot}001$). There was a significant effect of state on capture success of males (ANOVA, $F_2=7{\cdot}6$, $P<0{\cdot}012$). Capture success decreased from 10·5% on single males to 3·8% of attacks on mating pairs, and increased to 21·5% of attacks on struggling pairs. The decrease in capture success on mating males was not significant ($0{\cdot}1<P<0{\cdot}2$), but the increase on struggling males was significant ($P<0{\cdot}05$).

Capture of single gerrids always resulted in predation. Capture of mating or wrestling pairs usually resulted in predation of the female rather than the male, and never resulted in predation of both. Females suffered predation in 86% (SE=0·09) of captures of mating pairs and in 59% (SE=0·05) of captures of struggling pairs. This bias toward females in captures of mating pairs was clearly a positioning effect: backswimmers attack from below and male gerrids ride on top of females when mating. In those cases where the male was guarding the female, males would often release the female at the instant of capture by the backswimmer and therefore escape. In contrast, captures of copulating pairs always resulted in both male and female being dragged under the water by the backswimmer. This is because males in copula cannot instantly withdraw their genitalia and thus are attached to females for a few seconds. When mating pairs were captured, the male would usually soon float to the surface and escape. Capture of wrestling pairs rarely resulted in both individuals being pulled under water. Because wrestling pairs somersault and roll, the male would often be grasped by the backswimmer. In these cases it was the female that often escaped at the surface or soon floated to the surface.

I was not able to determine the proportion of time that gerrids were single, mating or wrestling. Therefore, I was unable to calculate the rate at which each class suffered attacks. However, observations suggest that attack rate was highest on wrestling pairs and lowest on mating pairs. It was clear that backswimmers were attracted to movement on the water surface. Unsuccessful attacks were often followed by one or more subsequent attacks by the same notonectid. This was particularly apparent on wrestling pairs because they were generally less responsive to attacks than either single or paired gerrids. Wrestling is vigorous, thus disturbance at the water surface was high. On the other hand, mating pairs appeared to reduce movement.

Females represented 51·8% (SE=2·8) of the total mortality in these experiments, despite an available sex ratio of 2:1. There was no significant difference between this value and the expected value of 33·3% (chi-squared).

DISCUSSION

These experiments demonstrate that components of the mating behaviour of *G. buenoi* increases predation risk to both sexes. Mate searching by males increases risk to males and all of the major components of mating behaviour appear to increase risk to females. These components include: (1) harassment by males, (2) pre-mating struggles, where females attempt to repel male mating attempts, and post-mating struggles, where females attempt to dislodge guarding males and (3) mating, which includes copulation and guarding.

Mating Costs

Backswimmers prey more efficiently on mating female water striders than on single female striders. The more than doubling in the susceptibility of female striders to predation results from their reduced speed and agility when burdened with a male. The response of gerrids to backswimmer attack was to leap off the water surface and/or skate rapidly from the scene. Both Arnqvist (1989a) and Fairbairn (1993) have shown that female mobility is decreased when carrying males. Female sensitivity to this risk of predation offers one explanation for the retreat of mating *G. buenoi* to refuge (Rowe 1992a) and for the decreased mating frequency and duration observed in *A. remigis* in the presence of predacious fish (Sih et al. 1990).

Females appear to adjust their behaviour when mating in such a way that predation rates are probably less than those expected from the capture success of backswimmers alone. In the experiment on backswimmer capture success, backswimmers oriented to disturbance of the water surface. Perhaps in response to their abilities, female gerrids appeared to reduce their skating rate in the presence of backswimmers. Sih et al. (1990) have similarly shown that female *A. remigis* reduce their rate of movement in the presence of sunfish predators. In the wild, mating females further reduce exposure to predation by moving to the refuge of floating vegetation (Rowe 1992a) and this is reflected by the greater use of refuge than single females (this study).

Costs of Mate Choice

Arnqvist (1989b) has shown that pre-mating struggles function in mate choice by females. Here I have demonstrated that these struggles (pre- and post-mating) increase predation risk to females. Capture success was more than doubled on both sexes when wrestling compared with being single (Table II). Capture success alone probably underestimates the risk to wrestling females. Wrestling is vigorous, including somersaulting (Rowe 1992a) and such disturbance attracts backswimmers. Most pre-mating struggles result in the escape of the female and these struggles are significantly longer than those that result in mating (Rowe 1992a). When female water striders are reluctant to mate, mean struggle duration increases (Arnqvist 1992c; Rowe 1992a), and as a result the degree of non-random mating of males increases (Arnqvist 1992a, b; Sih & Krupa 1992). Only select male phenotypes appear able to overcome lengthy female struggles (Arnqvist 1989b). My data show that female reluctance, the mechanism of mate choice, comes at a cost of increased predation risk to females. In short, the longer a female struggles the more likely she is to bias mating success toward preferred phenotypes and the more likely she is to be preyed upon.

Costs of Harassment

Harassment of females by males is frequent in the wild (up to 47 mating attempts/h, Rowe 1992a). Female water striders actively avoid male advances by skating from the scene and retreating to refuge (Krupa et al. 1990; Rowe 1992a). This mate searching in males and escape by females appears to be costly. Both entail increased movement rates, which attract backswimmers, and this is reflected in the increased movement rates of both sexes when held together relative to when held separately (Table I). Male movement rates were also significantly higher than female rates in the laboratory, and males spend significantly more time in the risky open water habitat in the wild. These results almost certainly reflect mate searching behaviour by males rather than increased foraging rates. Females' foraging needs are intuitively expected to be higher because they are producing eggs, and these needs are reflected in feeding rates by females that are equal or higher than in males (Rowe 1992a). Finally, males that actually find a female and attempt to mount her, are at increased risk of detection and capture by backswimmers. Like females, males are at greater risk of capture by backswimmer attacks when struggling than when single, and struggles probably increase attack rates (see above). Predation risk associated with mate searching by males appears to be relatively common (Magnhagen 1991).

Economics of Mating Behaviour and Sexual Selection

The results of the current study support the view that variation in mating behaviour of females, and as a result sexual selection on males, reflects variation in the strength of natural selection acting on female reluctance to mate (Arnqvist 1992a, b, c; Rowe 1992a; Sih & Krupa 1992). Costs of mating include increased predation risk (Fairbairn 1993; this study) and decreased mobility and foraging (Arnqvist 1989a; Rowe 1992a; Fairbairn 1993). However, females choosing to avoid the costs of mating must engage in costly pre-mating struggles (increased predation, this study). Therefore, females must strike some balance between the costs associated with mating and those of avoiding mating. Thus female reluctance is the relevant target of natural selection. When either the costs of mating or the costs of not mating are experimentally varied, female mating behaviour changes in the direction predicted by this economic view (Arnqvist 1992c; Rowe 1992a). For example, an experimentally increased rate of harassment of females increases the cost of remaining single, and as predicted, mating frequency and duration increased (Rowe 1992a). Non-random mating success of males appears to be a by-product of adaptive female reluctance and therefore, sexual selection on male phenotypes may best be understood as a pleiotropic effect of natural selection on female reluctance to mate. This system is similar to that described as 'sensory exploitation' because the behaviour used in mate choice (the struggle) has a primary function and perhaps evolved in another context (Kirkpatrick & Ryan 1991; Ryan & Keddy-Hector 1992).

Predation Risk, Survival and the Mating System

The contribution of each of these risks to survival patterns in the wild is not easily predicted. Most components of the mating behaviour of *G. buenoi* appear to be plastic and responsive to environmental variation (Rowe 1992a). As such, the contribution of each component of mating behaviour to mortality is expected to depend strongly on the particular environmental context. For example, mating *G. buenoi* females often retreat to refuge (Rowe 1992a). In habitats with abundant refuge, low mortality rates resulting from mating may be expected. However, in habitats where refuge is sparse, predation risk to females when mating may contribute significantly to survival patterns. Indeed, the scarcity of refuge in the studies of Arnqvist (1989a) and Rowe (1992b) may have contributed to the observed female bias in mortality rates. Moreover, variation in predation risk may actually manifest itself as variation in another component of fitness (e.g. growth) rather than survival (McNamara & Houston 1987; Ludwig & Rowe 1990). Therefore, whether predation risk actually results in elevated mortality rates is by no means certain. None the less, predation risk associated with the components of mating will play a real role in structuring the mating system, individual variation within that system, and sexual selection.

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