

## Convenience polyandry in a water strider: foraging conflicts and female control of copulation frequency and guarding duration

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**Abstract.** The mating behaviour of the water strider *Gerris buenoi* Kirkaldy was investigated in the field and laboratory. The conflict between foraging demands and mating was examined and the convenience polyandry hypothesis for superfluous mating was tested directly. Mating is multiple, females are reluctant, males are persistent and mating consists of a period of copulation followed by a guarding phase in which the male and female remain in tandem without genital contact. Males make frequent attempts to mate with females that often lead to vigorous struggles initiated by the females. All matings were terminated with a struggle initiated by the female that continued until males were dislodged. Field data support the hypothesis that mating conflicts with foraging. Females occupied with prey offered little resistance to male suitors and guarding durations were significantly longer when females were consuming prey or had fed recently. To test the hypothesis that females were more willing to mate when foraging demands were reduced, mating behaviour of bugs under different feeding regimes were compared. Female hunger reduced mating frequency 50% in the laboratory and male hunger had no effect. These data demonstrate that mating conflicts with foraging by females and that females appear to vary mating behaviour according to this conflicting demand. The convenience polyandry hypothesis predicts that females will accept superfluous copulations when the costs of repelling male mating attempts (remaining single) are greater than the costs of mating. To test this hypothesis, mating behaviour was compared under two sex ratios (1:1 and 3:1), where harassment of females and thus the costs of repelling males was expected to be higher in the male-biased treatment. Female mating activity, frequency and duration all increased significantly under a sex ratio of 3:1. In the male-biased treatment, harassment of females by males increased significantly and both mating activity and frequency were a positive function of harassment rate. Increased mating frequency resulted from an increase in the proportion of mating attempts that led to mating. Pre-mating struggles that led to mating were about one-quarter the duration of those that did not. Therefore, increased mating frequency under high harassment rate resulted from a decrease in female reluctance to mate. There was no treatment effect on the duration of post-mating struggles, indicating that increased guarding duration observed under the male-biased sex ratio resulted from a female decision to postpone dislodging the male. These results demonstrate a strong degree of female control over most components of mating and support the convenience polyandry hypothesis for superfluous mating.

The economics of multiple mating has attracted considerable interest (Daly 1978; Walker 1980; Thornhill & Alcock 1983). The costs of mating to females can be divided into two classes; costs of mating itself and the costs associated with repelling males. Costs of both classes may include risk of predation and loss of time and energy (devoted to or lost to either activity). Thus, mating may conflict with other activities such as foraging and predator avoidance, and females, therefore, face trade-offs when deciding to repel suitors or accept them. Few studies

have examined mating in light of such conflicting demands.

Multiple mating by males can have a direct positive effect on fitness; reproductive success of a male is often limited by the number of ova he can fertilize. On the other hand, reproductive success of females is unlikely to be limited by sperm and thus additional mating is less likely to have a direct positive effect on their fitness. Nevertheless, there are several potential indirect benefits of mating for females. These include parental investment by males (e.g. nuptial feeding and nutritional

resources passed with sperm), reduced predation risk and increased genetic diversity of offspring (see reviews in Walker 1980; Thornhill & Alcock 1983; Smith 1984). Here multiple mating is viewed as advantageous to females if benefits of mating are greater than costs. If females can control mating, then they should mate at a rate that minimizes these costs.

Alternatively, females may accept superfluous mating to reduce costs of harassment by male suitors (e.g. Walker 1980; Parker 1984; Wilcox 1984); females may accept additional mating if the cost of repelling amorous males is greater than the cost of accepting them. Thornhill & Alcock (1983) refer to such mating systems as 'convenience polyandry'. Although it is intuitive that females will mate when the costs of repelling males becomes high, to my knowledge there have been no attempts to test the hypothesis of convenience polyandry. Furthermore, a suite of testable predictions arising from this idea has not been formulated.

In their discussion of convenience polyandry, Thornhill & Alcock (1983) focus on the proposition that males can make it so costly (direct costs) for females to repel their amorous attempts that females will mate out of convenience. For example, the act of preventing copulation may have a direct energetic cost. As costs are elevated, it will become adaptive for females to accept the male. Testing this hypothesis seems difficult since a simple method of manipulating direct costs of male mating attempts is not apparent. Alternatively, repelling males may have some indirect costs, such as increasing predation risk, and females may accept superfluous copulations when risk is elevated. However, interpretation of such a test would be confounded if costs of mating and repelling males were analogous: if both mating and repelling males increased predation risk, then females may be more or less likely to mate when predation risk is increased.

A second set of indirect costs of repelling amorous males are those incurred after the physical interaction with the male. One consequence of successfully repelling a male is exposure of single females to further costly harassment. Therefore, the costs of successfully repelling a male should be a positive function of harassment rate. Manipulation of harassment rates is relatively easy and will not be confounded in cases where costs of repelling males and mating are analogous. Simple methods to increase harassment rate include: (1) removing

refuges for females from males and (2) increasing density and thus encounter rates between the sexes or (3) biasing the sex ratio towards males and thus the encounter rate of females with males. The overall prediction is a positive relationship between harassment rate and mating activity of individual females. However, such a relationship may result without any response of females to the manipulation. Mating activity may increase without increased female receptivity, because an increased rate of male mating attempts alone could produce such a result. Therefore, a demonstration that females mate for convenience should include a positive relationship between harassment rate and female receptivity to mating.

Water striders (Heteroptera: Gerridae), are one of the few groups where variation in mating behaviour has been studied in response to variation in conflicting demands. Water striders mate multiply, despite probable energetic costs and predation risks to females (e.g. Andersen 1982; Wilcox 1984; Arnqvist 1989b). Sperm is stored, last male sperm precedence occurs and sperm is transferred rapidly relative to total mating durations (Andersen 1982; Arnqvist 1988; Rubenstein 1989). Therefore, most mating may be considered superfluous to the female. Males ride on the back of females during copulation, and may remain in tandem, guarding the females after copulation has ceased (Andersen 1982; Wilcox 1984; Arnqvist 1988). Rubenstein (1984) and Wilcox (1984) hypothesized that females of the lotic water strider *Gerris remigis*, may actually benefit from long matings despite a probable cost of carrying males. Females in tandem are harassed less by other males and are therefore able to spend more time foraging and foraging success is nearly tripled (Rubenstein 1984; Wilcox 1984).

In one laboratory study of *G. remigis*, female hunger level had no effect on mating duration, but duration was extended when sex ratio was male biased (Clark 1988). He concluded that sperm competition, not Wilcox's enhanced foraging hypothesis, accounted for variation in mating duration. However, in a similar study, Sih et al. (1990) found that mating duration of *G. remigis* was reduced when males and females were simultaneously deprived of food. The latter authors concluded that mating duration was reduced because mating conflicted with feeding by males; males in contrast to females do not feed in tandem. Interpretations offered by Clark (1988) and Sih

et al. (1990) imply that males control mating duration, despite a lack of information on control of either mating frequency or mating duration in water striders. Therefore, the role of food in the mating behaviour of *G. remigis* remains ambiguous.

In contrast to lotic Gerrids, foraging by females of lentic (still water) species is less likely to be enhanced by males in tandem: food in lentic habitats is not concentrated in patches (e.g. Vepsäläinen & Nummelin 1985b; Spence & Wilcox 1986). Thus, in pond species, foraging in tandem is probably less efficient and may increase the risk of predation (Vepsäläinen & Nummelin 1985b; Arnqvist 1989b). Therefore, mating is predicted to conflict with foraging. However, the role of food in mating behaviour of lentic water striders has not been addressed.

In the present study, I examine mating behaviour of the lentic water strider *Gerris buenoi* Kirkaldy in light of conflicting demands and directly test the convenience polyandry hypothesis. Field and laboratory studies are used to determine the effect of variation in both costs of mating and repelling males (e.g. not mating; remaining single) on mating behaviour. First, I describe mating behaviour in the field with reference to foraging. Second, I test the following hypotheses: (1) mating conflicts with foraging and that variation in mating behaviour reflects variation in foraging demands of females, (2) mating activity (frequency  $\times$  duration) is a positive function of the rate of harassment by males, (3) females play a significant role in determining mating frequency and duration, and (4) female receptivity to mating is a positive function of harassment rates.

## METHODS

The life history and habitat use of *G. buenoi* have been well described (Spence & Scudder 1980; Spence 1989). *Gerris buenoi* is partially bi-voltine and is common to both temporary and permanent habitats throughout much of North America. Macropterous adults emerge from overwinter diapause in early spring to reproduce. Females continue to mate throughout post-diapause life (a few months) and oviposit approximately daily (Spence 1979; Rowe & Scudder 1990). All bugs used in the present work were macropterous and had diapaused.

## Behaviour in the Field

Field observations were conducted at Shallow Pond in the University of British Columbia Botanical Gardens, during June and July of 1990. Shallow Pond is a small (12  $\times$  8 m) permanent pond surrounded by gardens and lacking shading from trees. Therefore, the entire surface of the pond can be surveyed from the shore. During the study period, about 25–50% of the pond surface was littered with debris (floating and emergent vegetation). *Gerris buenoi* is the numerically dominant water strider throughout the season in this pond. *Gerris incognitus*, *G. incurvatus* and *Limnoporus notabilis* were also present. Sex ratio in this and nearby ponds varies from male to female biased (unpublished data).

I used several methods to quantify behaviour. I made all observations from the shoreline with a pair of binoculars, between 1100 and 1700 hours. During a 5-day period, focal animal observations were made on 27 females. Single females were observed continuously for a total of 10 min or until lost from sight. If mating occurred during the sampling period, observation continued until mating terminated. I recorded the number of lunges by males at females (attempts), the female's reaction and the durations of any ensuing pre-mating struggle, copulation and guarding, and the number of attempts by males to copulate or interrupt these pairs. Five matings were observed during the focal animal study. By searching the pond for struggling pairs I was able to time an additional 28 matings. In five of these cases I came across pairs during copulation and four cases during guarding. In these cases I assumed that my observation started half way through the phase in question. On several occasions, I surveyed the pond to determine whether tandem pairs were in the open water or on floating debris. In a final survey, I scanned the pond to determine the ratio of feeding to non-feeding males, females and pairs. In summary, location only of 170 pairs was determined, location and use of prey was determined for an additional 73 pairs and, location, prey use and foraging was determined for an additional 33 pairs. Throughout the study, I recorded information on foraging, feeding and oviposition behaviour. For the purposes of clarity and brevity, I will refer to consuming prey as 'feeding' and, searching for and capturing prey as 'foraging'.

### **Effect of Hunger and Mating Behaviour**

I determined the effect of hunger on both sexes by comparing mean mating activity, frequency and duration of matings in replicate experimental containers. Plexiglas pools had a water surface area of 0.5 m<sup>2</sup> and depth of 3 cm. Water striders were collected from J. K. Henry Pond at the University of British Columbia Botanical Gardens and held for 72 h in large plastic wading pools in the laboratory until 24 h prior to the experiment, at which time the sexes were separated and the bugs individually marked with acrylic paints. Food (frozen fruit flies) was provided *ad libitum* until 6 h prior to the experiment. At that point, water striders were further divided into 'fed' and 'unfed', males and females. Unfed water striders were deprived of food for the remaining 6-h period, while fed bugs continued with abundant food.

I assigned six males and six females to each of nine pools (three replicates for each of three treatments). Treatments were the 'control' (both sexes fed), 'male hunger' (males unfed, females fed) and 'female hunger' (males fed, females unfed). At 10-min intervals each pool was visited and the activity of each individual was recorded as either mating or non-mating. The experiment continued for 4.5 h. At that point, the first mating of any female had been terminated, although some females had not mated once and others had mated more than once. Duration of a mating was estimated from the number of consecutive visits that a pair was seen in tandem.

Each pool was treated as a replicate for statistical analyses. Mating activity was the proportion of time females were mating and was calculated as the sum of the number of mating pairs on each of 27 visits divided by the potential number of matings (number of females  $\times$  27 visits). Mating frequency was the total number of matings that occurred in each replicate divided by the number of females present. Mating duration was calculated as the mean duration of matings that had occurred in each replicate. Only matings in which neither individual had mated previously during the experiment were used for analysis of mating duration (independent matings as in Clark 1988). Nevertheless, results were similar if all matings were included.

### **Sex Ratio and Mating Behaviour**

In a second experiment I determined the effect of sex ratio on mean mating activity, mating frequency

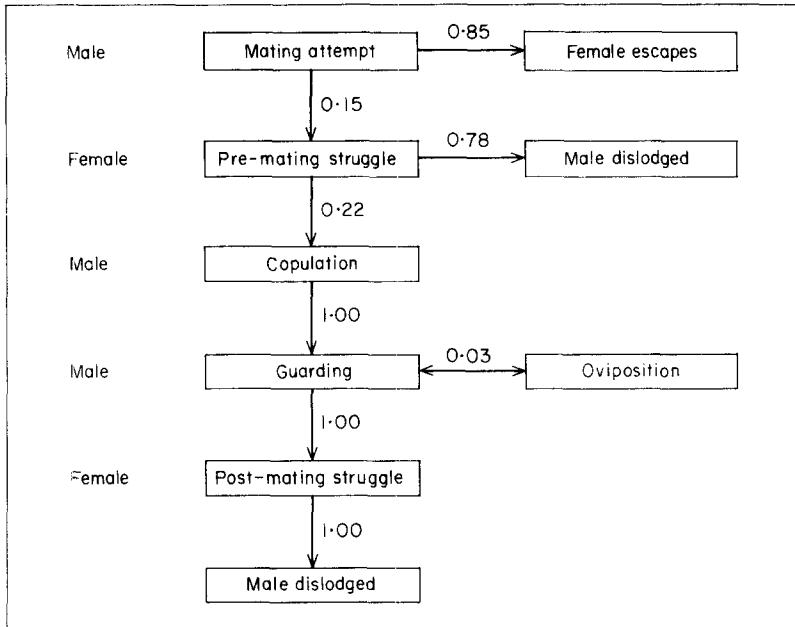
and durations of copulation and guarding in replicate experimental pools. I set up four replicate pools containing 12 water striders for each of two treatments; the two treatments were male:female sex ratios of 1:1 and 3:1. Details of this experiment and analyses are as in the previous experiment, except that I determined whether pairs were copulating (genital contact) or guarding (no genital contact) on each visit.

### **Harassment and Control of Mating Activity**

In a third experiment, I determined the effect of sex ratio on several dependent variables chosen to indicate which sex controls mating frequency and duration. This experiment focused on detailed components of mating behaviour that could not be addressed in the first experiment. Dependent variables were frequency of attempted matings by males on females, proportion of attempts resulting in pre-mating struggles, duration of these struggles, proportion of struggles resulting in matings, mating activity and duration of post-mating struggle. Because of the high density of bugs in these pools it was difficult to distinguish lunges of males at females, as I had in the field. Therefore, I defined a mating attempt as a deliberate lunge at females by males that resulted in contact. Hence harassment rate was underestimated in the laboratory relative to the field. I similarly recorded the number of male attempts on other males and on mating pairs.

Observations on single pools were made continuously for 45 min. Each pool contained 12 bugs at sex ratios of 1:1 or 3:1. Males were marked with acrylic paint to aid in identification of the sexes. Events were recorded by type and time. Pre- and post-mating struggles were recorded to the second except in cases where struggles lasted less than 3 s, in which case all were given values of 1.5 s. The experiment was repeated four times on 12 June and four times on 13 June, with alternation of treatments. Untested water striders were used in each replicate. Sexes were separated in holding pools 16–24 h prior to experiments. Remaining experimental conditions were as in the previous experiments.

All comparisons of means were made on log-transformed data, except for proportions which were arcsine transformed. Unless otherwise stated, I used *t*-tests to test for significance of differences between means.



**Figure 1.** The mating sequence of *G. buenoi*. Numbers next to arrows are proportions estimated from field observations and reset to 1.00 after each outcome. Left column indicates which sex initiates the action described to the right. Further details are given in the Methods and Results sections.

## RESULTS

There are four phases to mating in *G. buenoi*: pre-mating, copulation, guarding and post-mating (Fig. 1). The pre-mating phase is initiated by males lunging at the female. Males that successfully contact females attempt to grasp the female's thorax with their forelegs and insert their genitalia. Females respond by rearing up on their mid-legs and somersaulting in an attempt to dislodge males from their back. Females use their forelegs to break the male's grasp of their abdomen. The copulation phase begins when males successfully insert their genitalia and struggling desists. After several minutes of copulation, a guarding phase is initiated when the male withdraws his genitalia but remains on top of the female. I will refer to the combination of copulation and guarding phases as mating. The post-mating phase consists of a struggle initiated by females, similar to struggles in the pre-mating phase, that terminates mating. A second male would often attempt to copulate or perhaps interrupt mating pairs ( $\bar{X} \pm SE = 2.2 \pm 0.51$  attempts per mating,  $N = 20$ ). However, these attempts were usually short lived; males mounted the pair, occasionally probing with their genitalia, and then quickly dismounted. Attempts by second males

usually elicited little response from mating pairs and never resulted in take-over or interruption.

### Pre-mating Phase

Females spent much of their time avoiding amorous males. In the focal individual observations, a given female was lunged at by males about 47 times per h. Most of the 147 attempts recorded were unsuccessful (97%), usually contact is not made (females leap vertically and/or skate off) and few attempts result in pre-mating struggles (15%). Mean duration of pre-mating struggles was 7.3 s and only 22% of struggles resulted in a mating (Fig. 1). Although sample size was small, there was no evidence that the probability of a male copulating resulted from that particular male's ability to withstand struggles. The longest pre-mating struggle observed in the field was 63 s and did not lead to a copulation. All others were less than 15 s.

### Food and Mating

Foraging males and females skate about searching for living and dead insects trapped on the water surface. Prey location appears to be both

visual and tactile. Water striders often approach inanimate (often non-food) items and probe them with their mouthparts, but are particularly attracted to prey items struggling to escape the water surface. Bugs pick up smaller prey items (e.g. midges) and skate off to floating debris to feed. Larger prey (e.g. damselflies) that can not be transported are fed upon where they were found. Large prey are often fed upon by several individuals, but are rare in the diet. Females appeared to spend more time feeding than males. In the feeding survey, single females were found feeding almost twice as often as males (16.3%,  $N=92$  and 9.4%,  $N=85$  respectively), but this difference was not significant ( $0.25 > P > 0.10$ , contingency table test).

Mating conflicts with foraging of both males and females. Upon commencement of copulation, females skate to or remain on floating debris and become inactive: 89% of 276 mating pairs, located throughout the study, were inactive on floating debris. Some mating females did dart out from a resting spot to capture prey items struggling on the water surface nearby. However, this was observed in only three of the 33 mating pairs where behaviour during mating was observed. Although females often feed while mating, they are consuming prey captured prior to initiation of mating (see below). I never observed a male feeding while mating.

Females are more willing to mate while feeding than while undertaking other tasks such as foraging for prey, grooming or resting. Of five matings recorded in the focal individual observations, three occurred after females had captured and were feeding on a prey item. Of the 33 complete matings observed, 36% of these females had prey items in their grasp at some time during the mating. This is probably an underestimate, since very small prey items may have been missed in these observations. In the feeding survey, 29% ( $N=73$ ) of mating females were feeding while only 16% ( $N=92$ ) of single females were feeding and this difference approaches significance ( $0.01 < P < 0.05$ , contingency table test). On several occasions, I placed a freshly killed damselfly on the water surface and observed gerrid behaviour around it. Within a few minutes, both males and females could be seen feeding upon it. Often males approaching the carcass would mount feeding females and females offered little or no resistance.

Variation in mating duration in the field was high, ranging from 4.0 to 61.5 min. Most of this

variation reflected variation in duration of guarding (range = 0.0–54.4 min), not copulation (range = 4.0–14.0 min). Females that have fed during copulation are guarded significantly longer than those that have not ( $P < 0.01$ ). Mean ( $\pm$ SE) guarding duration was  $16.4 \pm 1.50$  min in cases in which females had fed and  $0.5 \pm 0.04$  min in those that had not. However, copulation duration did not differ between females that had fed and those that had not ( $P > 0.1$ ). Mean ( $\pm$ SE) copulation duration was  $7.1 \pm 0.33$  min for females that had fed and  $7.7 \pm 0.16$  min for those that had not.

### Post-mating Phase

In all cases matings were terminated during the guarding phase and after the female had initiated a post-mating struggle. Males never simply dismounted. Post-mating struggles, once initiated, continued until the male was dislodged. I did not attempt to time these struggles, however, they appeared to be about the same duration as pre-mating struggles. Often the switch from copulatory to guarding phase occurred when the female had dipped the tip of her abdomen under the water surface.

### Oviposition and Territoriality

Oviposition in this species is difficult to observe. Females dip their abdomen under the water and oviposit one or several eggs on floating debris, such as algal mats, leaves and other floating vegetation. They rarely oviposit while mating; only one of 33 females that I monitored during mating oviposited and only two of the 25 ovipositions I observed throughout the study occurred with males in tandem. Furthermore in the remaining 23 events, there was no evidence of males non-contact guarding nearby. I saw no evidence of territoriality by males or females. Both males and females roamed over much of the pond and I never observed fighting or other aggression between females. Although males often attempted to mount one another, they did not fight on contact or chase one another. Males commonly attempted to mate other males, conspecific males and females, and even inanimate objects.

### Effect of Hunger on Mating

Results of the laboratory test on the effect of hunger on mating behaviour showed that female

**Table I.** Mean (SE) effect of hunger on mating behaviour of *G. buenoi*

Treatment	Mating		
	Activity	Frequency	Duration
Female fed– males fed	0.42 (0.10)	1.71 (0.45)	55.33 (6.49)
Females fed– males unfed	0.45 (0.05)	2.23 (0.53)	61.67 (7.92)
Female unfed– males fed	0.20 (0.03) *	0.85 (0.18) **	57.67 (6.36)

Mating activity: mean proportion of time females mate; mating frequency: mean number of matings per female throughout the experiment; mating duration: duration (min) of the average mating, comprising both copulation and guarding phases.

\* $P < 0.01$ ; \*\* $P < 0.01$ , ANOVA for treatment effect comprising means between rows ( $N = 3$  for all means).

hunger had a strong effect on mating behaviour and male hunger had no effect (Table I). Hungry females spent 55% less time mating than recently fed females. This was largely owing to a significant 53% decrease in mating frequency. I compared treatments with an analysis of variance and where significant treatment effects were detected, I partitioned the treatment sum of squares to compare the effects of female hunger and male hunger (Snedecor & Cochran 1967, pp. 308–310). There was a significant overall treatment effect on mating activity and frequency, but not duration (Table I). A comparison of the female hunger treatment with the remaining two treatments revealed a significant effect of female hunger on both mating activity ( $P < 0.05$ ) and frequency ( $P < 0.01$ ). A comparison of control and male hunger treatments on mating activity and frequency was not significant ( $P > 0.50$ ). Variation in duration of the 87 observed individual mating events was high (10–140 min).

### Sex Ratio

Sex ratio had a strong effect on most measured aspects of mating behaviour (Table II). Mating activity increased 64% and mean mating duration increased about three-fold, from 34.2 to 100.7 min, when the sex ratio was increased from 1:1 to 3:1. Most of this increase in mating duration was due to an increase in guarding duration (60.5 min),

although copulation duration also increased (6.0 min; Table II). The 97 individual mating events ranged from 10 to 240 min in duration.

Mating frequency decreased significantly from 4.6 to 3.5 matings per female when sex ratio was male biased (Table II). This was an unexpected effect that may result solely from the increase in mating duration, since some matings continued over much (up to 89%) of the duration of the experiment. To disentangle mating frequency from duration, I compared the proportion of females that had commenced mating within the first 30 min of the experiment. Viewed in this manner, mating frequency increased when sex ratio was male biased from 54 to 92% of females mating within the first 30 min of the experiment (Table II).

### Harassment and Female Control

As expected, increasing sex ratio from 1:1 to 3:1 resulted in a significantly increased rate of male harassment of females. Single females were exposed on average to 11.75 mating attempts per hour at a sex ratio of 1:1 and 29.25 at 3:1 (Table III). Related to this increase in harassment rate was a significant increase in mating activity and frequency (Table III, Fig. 2a, b). Increased mating activity and frequency was not solely due to an increased harassment rate. The proportion of attempts by males that resulted in copulation more than doubled under male biased sex ratio (Table III) and was a positive function of harassment rate (Fig. 2c; the number of attempts per single female hour). Success rate was an increasing function of the rate of male attempts on females (Fig. 2c). Differences in success rate of males did not appear to result from differences in effort by males in pre-mating struggles in response to sex ratio. Successful struggles were less than one-third the duration of unsuccessful struggles in both treatments (Table IV) and successful and non-successful pre-mating struggles were actually of slightly shorter duration in the male-biased treatment (Table IV). Thus, increases in the bias of sex ratio towards males led to increases in harassment rate, and in turn, to a decrease in female reluctance.

Males did not appear to give up in their attempts to gain or retain a mating. All observed terminations of matings ( $N = 17$ ) were initiated by females attempting to dislodge the male after the male had withdrawn his genitalia. Once an attempt to dislodge the male was initiated, the struggle was

**Table II.** Mean (SE) effect of sex ratio on mating behaviour of *G. buenoi*

Sex ratio	Mating activity	Mating frequency	Early frequency	Duration (min)		
				Mating	Copulation	Guarding
1:1	0.51 (0.04)	4.65 (0.49)	0.54 (0.08)	34.25 (6.58)	11.75 (0.63)	22.50 (6.65)
3:1	0.85 (0.05) *	3.50 (0.32) NS	0.92 (0.08) *	100.75 (20.26) *	17.75 (0.75) **	83.00 (20.03) **

Early frequency refers to the mean proportion of females mating within the first 30 min of the experiment. Other terms are as in Table I.

\* $P < 0.05$ , \*\* $P < 0.01$ , *t*-test for sex ratio effect comparing means between rows ( $N = 4$  for all means).

**Table III.** Mean (SE) effect of sex ratio on mating behaviour of *G. buenoi*

Sex ratio	Mating activity	Mating frequency	Harassment rate	Success rate
1:1	0.19 (0.04)	0.66 (0.18)	11.75 (1.26)	0.09 (0.02)
3:1	0.66 (0.10) **	1.25 (0.09) *	29.25 (4.00) **	0.21 (0.04) *

Harassment rate: number of male attempts to copulate with females per single female hour (see Methods); success rate: proportion of mating attempts that resulted in copulation; other terms are as in Table I.

\* $P < 0.05$ ; \*\* $P < 0.01$ , *t*-test for sex ratio effect comparing means between rows ( $N = 4$  for all means).

continued until males were dislodged. There is no evidence that males put more effort into frustrating the female's attempts at dislodgement when sex ratio was biased toward males. Post-mating struggles were longer than pre-mating struggles and there was no difference in post-mating struggles between treatments (Table IV). Therefore, longer guarding durations in the male-biased sex ratio in the prior experiment, appeared to result not from increased efforts by males but from a lack of attempts to terminate mating by females. The longer duration of post-mating struggles relative to pre-mating struggles was probably due to males having gained a secure grasp of the female in the

former case, rather than any increased effort on their part.

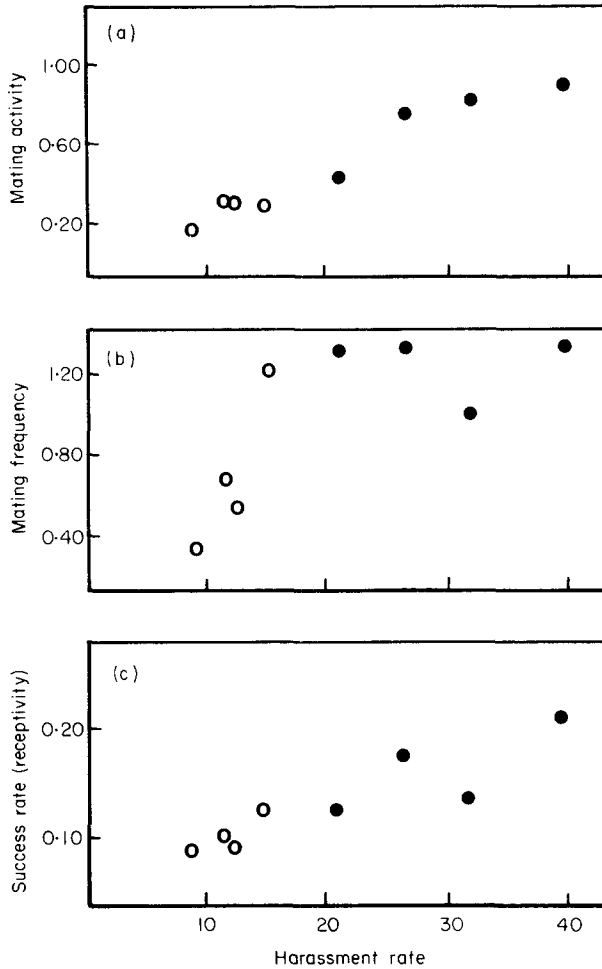
## DISCUSSION

### Convenience Polyandry

Several authors have suggested that females accept superfluous matings because of the high costs of harassment imposed by male suitors ('convenience polyandry' sensu Thornhill & Alcock 1983; see also Walker 1980; Parker 1984). To my knowledge, my results with *G. buenoi* represent the first experimental evidence of convenience polyandry. The cost of repelling a male mating attempt was manipulated by increasing the frequency with which single females were harassed. Female mating activity more than tripled when the cost of repelling males was increased: females became more receptive to mating when harassment rate by males was increased.

As expected, under a male-biased sex ratio harassment rate and mating frequency increased (Tables II, III and Fig. 2b). The increase in mating frequency was not because of more frequent encounters with amorous males; rather, the proportion of male mating attempts that resulted in copulation was a positive function of harassment rate (Fig. 2c). Furthermore, increased success of mating attempts was not because of an increased vigour on the part of males attempting to mate, but because of an increase in female receptivity. Pre-mating struggles resulting in copulation were significantly shorter than those that did not, and there was no effect of treatment on the duration





**Figure 2.** The effect of male harassment rate on female mating activity (a), mating frequency (b) and receptivity (c). Harassment rate is the number of male mating attempts per single female hour; female receptivity is the proportion of male mating attempts per female that resulted in mating. ○: sex ratio of 1:1; ●: 3:1. Coefficients for correlations between harassment rate and mating activity ( $r=0.97$ ), mating frequency ( $r=0.72$ ) and success rate ( $r=0.92$ ) were all significant ( $P<0.01$ ;  $N=8$ ).

of successful and unsuccessful mating attempts. Therefore, the observed increased mating frequency resulted from a higher proportion of short (successful) pre-mating struggles when harassment rate was increased. In summary, females were more receptive to mating when harassment rate and thus the costs of not mating were increased.

Wilcox (1984) suggested that female water striders would accept longer mating durations if male harassment rates were high. My results support his hypothesis. Mating durations (copulation plus guarding) were about three-fold higher at a 3:1 than at a 1:1 sex ratio (Table II) and increased

mating durations were correlated with increased harassment rates at the 3:1 sex ratio (Table II, III). Similarly, mating durations of *G. remigis* were increased at a sex ratio of 3:1 relative to 1:3 (Clark 1988). Although Clark (1988) did not measure male harassment rate, it is expected to be higher (per female) when sex ratio is male biased.

Several studies have reported increased copulation or guarding durations when sex ratio is male biased (McLain 1980, 1989; Sillén-Tullberg 1981; Clark 1988; Telford & Dangerfield 1990). Results of these studies were interpreted as male responses to increased male competition (but see Moore

**Table IV.** The mean (SE) effect of sex ratio on the duration of pre- and post-mating struggles

Sex ratio	Duration of struggle (s)		
	Pre-mating		Post-mating
	Successful	Unsuccessful	
1:1	8.8 (0.7)	34.4 (1.8)	64.2 (16.9)
3:1	7.5 (1.0)	31.3 (5.0)	84.2 (12.4)
	NS	NS	NS

Successful struggles led to mating, unsuccessful struggles did not. Other terms are as in Table I.

\* $P < 0.05$ ; \*\* $P < 0.01$ ,  $t$ -test for sex ratio effect comparing means between rows ( $N = 4$  for all means).

1989). When sex ratio becomes male biased, sperm competition is intensified and pay-offs to guarding males should increase. However, my experiments revealed that females, not males, controlled guarding duration. Termination of all matings followed a post-mating struggle initiated by the female during the guarding phase. Males appeared to have little control over the outcome of female attempts to dislodge them. Post-mating struggles, once initiated, continued until males were dislodged. There was no evidence of males struggling more vigorously to remain on top of the female.

### Food and Mating

In contrast to earlier studies of lotic gerrids (Rubenstein 1984; Wilcox 1984; Vepsäläinen & Nummelin 1985a) my results indicate that mating conflicts with foraging by females in this lentic water strider. Upon commencement of mating, females typically skate to floating debris and then become inactive. There are several potential reasons for females to cease foraging for prey when mating. Carrying about a male is presumably energetically costly for female water striders and skating speed is reduced in *G. odontogaster* (Arnqvist 1989b). Furthermore, predation risk to females may be increased when in tandem. When male *G. odontogaster* are introduced to experimental pools containing predaceous backswimmers (*Notonecta* sp.), predation of females increased (Arnqvist 1989b). Backswimmers are a major predator of *G. buenoi* (Spence 1983, 1986). My

studies of predation by backswimmers, show that capture success of female gerrids is doubled when *G. buenoi* are in tandem (unpublished data). Backswimmers strike from below and floating debris represents a refuge for gerrids from predation. Female *G. remigis* become inactive and often attempt to crawl off the water surface when predation risk is experimentally increased (Sih et al. 1990). In summary, female *G. buenoi* probably retire to floating debris when mating to reduce energetic costs of skating in tandem and to reduce predation rates. Males do not feed while mating.

Results from the experimental manipulation of female hunger support the hypothesis that mating activity is influenced by the conflicting demand of foraging by females. Hungry females mated half as often as recently fed females and thus reduced time lost to mating by half (Table I). These results mirror preliminary experiments I undertook with *G. buenoi* and *G. incognitus* in which females were deprived of food for 18 h, rather than 6 h, and mating frequency was reduced by 80–90%. Although mating also conflicts with foraging by males, male hunger had no effect on mating activity, duration or frequency. These results provide another line of evidence for female control of mating frequency in *G. buenoi*. It is perhaps not surprising that females and not males respond to hunger. Food requirements and hence the value of foraging are probably much lower for males. Males appeared to forage less often in the field (this study), are smaller than females (Fairbairn 1990), and egg production rate by females is strongly limited by food in *G. buenoi* (Rowe & Scudder 1990) and other water striders (Kaitala 1987). Nevertheless, males may alter mating behaviour after some extended period of food deprivation.

Clark (1988) found no effect of food deprivation of female *G. remigis* on mating duration and did not report frequency. In contrast, Sih et al. (1990) showed that mating activity of *G. remigis* was reduced when both males and females were deprived of food and this was largely because of reduced mating duration. Sih et al.'s (1990) treatment was much more severe than mine; 24 h food deprivation versus 6 h. In addition, mean mating duration in control bugs was greater than 3.5 h for Sih et al.'s (1990) study compared to about 1 h for Clark's (1988) and the current study (Table I). Therefore, each mating in the former study represents a much higher cost in lost foraging time than those in the latter studies. Sih et al. (1990)

reported a 15%, statistically non-significant, decrease in mating frequency in hungry bugs. Interpretation of their frequency results may be confounded by the decrease in mating duration of hungry individuals. Such a decrease would lead to an increase in availability of single females relative to the fed treatments. Under equal availability of single females the effect on mating frequency may become significant. Perhaps the most significant difference between the studies of Clark (1988) and Sih et al. (1990) is that the former was carried out in running water and the latter in still water. In streams, females maintain territories and thus may accept mating to retain these territories independent of hunger (see below). In pools, *G. remigis* may behave more like *G. buenoi*, since maintaining a territory is unlikely to be profitable in still water.

Guarding duration is much greater when females are consuming prey. There are probably two reasons for this. Any attempt to dislodge the male may lead to the loss of that prey item. Prey items are grasped with the forelegs during feeding which are therefore unavailable to break the grasp of males. Furthermore, feeding females have no need to forage and hence the costs of mating to them are reduced. Guarding duration is also positively associated with the rate of male harassment (mating attempts) of females. This effect may explain greater mating durations in the laboratory experiment relative to field matings. Density of bugs and hence harassment rate was much greater in the laboratory than in the field (personal observation).

### Components of Mating and Female Control

Aspects of mating behaviour in *G. buenoi* are common to most water striders. They mate multiply, females are reluctant, males are persistent and ride on top of females during copulation and subsequent guarding (Andersen 1982). In *G. buenoi*, copulation is initiated by male attempts to mount the female followed by female attempts to dislodge them. Although common in water striders, the function of pre-mating struggles is unclear. They may be a form of mate selection or simply represent a general reluctance of females to mate. Male *G. odontogaster* which have longer abdominal grasping apparatus are better able to withstand attempts by females to dislodge them and have higher mating success (Arnqvist 1989a). These data lend support to the mate selection hypothesis in

*G. odontogaster*. Nevertheless, much of the variation in mating duration and frequency in *G. odontogaster* can be explained by a general reluctance of females to mate (Arnqvist 1992a). *Gerris buenoi* males do not possess an abdominal grasping apparatus and I found no evidence suggesting that success of mating attempts is related to a male's ability to withstand struggles to dislodge them.

Successful mating attempts appeared to result from a lack of female resistance. Females, currently occupied with a prey item offered little or no resistance. In the laboratory studies, struggles leading to mating were of significantly shorter duration than those that did not. Therefore, pre-mating struggles in *G. buenoi* appear to represent a general reluctance to mate and duration of these struggles is related to the degree of female reluctance. Nevertheless, mate selection may also motivate struggles to some degree. There is some evidence for homogamy in *G. buenoi* (Fairbairn 1988; unpublished data); perhaps females also adjust their level of reluctance according to their assessment of individual males.

Males do control copulation duration and vary it according to sex ratio (Table II). Copulation is terminated by males withdrawing their aedeagus, thus variation in copulation duration reflects a male decision. It is not entirely clear why males prolong copulation when sex ratio is male biased. Males may be responding to increased competition from other males. In several insect species, including water striders, sperm precedence increases with copulation duration (Thornhill & Alcock 1983; Parker 1984; Rubenstein 1989). Alternatively, males may increase copulation duration as a means of guarding. Females wait until males have terminated copulation before dislodging them. Perhaps dislodging males is too difficult when they have two points of attachment to the female (forelegs grasping the thorax and genitalia inserted). In the field, females often dipped their abdomen as if to oviposit. Perhaps as a response, males then often withdrew their genitalia as if to facilitate oviposition. Therefore, males face a trade-off in deciding whether to withdraw their genitalia: withdrawal of genitalia allows females to oviposit but also allows females to dislodge them. This behaviour remains intriguing and requires further study.

Termination of mating in water striders is also poorly understood. In *G. buenoi* all matings were terminated with a struggle initiated by the female. Similar results have been reported for *G. lateralis*

and *G. odontogaster* in Sweden (Arnqvist 1988, 1989a). It is unknown how mating is terminated in *G. remigis*, although this is crucial to questions concerning mating duration (Wilcox 1984; Clark 1988; Sih et al. 1990). Both female and male initiation of mating termination have been proposed or implied (op. cit.). If males simply dismount females then male control is clear, however if termination of mating is initiated by female struggles, then at least partial female control is suggested. My results suggest that female *G. buenoi* control mating duration. In both the laboratory and field, all matings were terminated with a struggle initiated by females. Most mating in the field is relatively short and, in the sex-ratio experiment I only quantified terminations of matings that had lasted 45 min or less. Therefore, longer matings may be terminated by the male. Nevertheless, in casual observation I have seen many long matings (> 1 h) terminated by females and I have never seen males simply dismount. Therefore, I conclude that the extension of the guarding phase when females are feeding results from a female decision to allow males to remain mounted.

Although, mate guarding duration in *G. buenoi* is determined by females, guarding may still be viewed as a male strategy to reduce sperm competition. Males continue guarding as long as females tolerate it. Males insure that their sperm is not displaced while guarding. Furthermore, in the field the guarding period of some portion of these males (albeit small) will continue over a bout of oviposition. Nevertheless, males may play some unseen role in determining guarding duration. For example, females may base part of their decision to terminate mating on male quality. In the current experiments males were randomly assigned among treatments, thus male quality cannot explain the observed variation between treatments.

### Comparison with Other Species

Mating and foraging behaviour in *G. buenoi* is less structured than it is in better studied water strider species. Behaviour of lotic species, such as *G. remigis* and *G. najas*, are characterized by food territoriality (Wilcox & Ruckdeschel 1982; Vepsäläinen & Nummelin 1985a; Blankenhorn 1991a, b). In streams food is localized by current, and territoriality is profitable (op. cit.). Maintenance of territories by females conflicts with repelling male suitors (Wilcox 1984). Thus, superfluous mating in this group may be a consequence, in part,

of female's need to maintain food territories. Territoriality also occurs in one group of lentic species, represented by *Limnoporus* spp. (Hayashi 1985; Vepsäläinen & Nummelin 1985b; Spence & Wilcox 1986). However, in this group territories are centred on oviposition sites and are maintained by males. Thus, females may mate to gain access to these oviposition sites. These two groups diverge in other life-history traits (reviewed in Fairbairn 1990). The first group are sexually dimorphic, primarily micropterous and common to permanent habitats, while the second are generally large bodied, less dimorphic, macropterous, univoltine and common to temporary habitats. *Gerris buenoi* shows neither food nor oviposition site territoriality. *Gerris buenoi* belongs to a third group of water striders that contains members of the sub-genus *Gerris*. They are small bodied, highly dimorphic, partially micropterous and partially bivoltine. Mating behaviour of *G. buenoi* may be representative of this group.

*Gerris odontogaster* appears to be morphologically and ecologically similar to *G. buenoi* (Arnqvist 1989a). In a recent study of mating behaviour in this species, Arnqvist (1992a, b) found that mating frequency and duration both increased and female reluctance to mate decreased when sex ratio was biased toward males and when density was increased. These results suggest that the mating system of *G. odontogaster* is also similar to *G. buenoi*. Although Arnqvist did not measure harassment rate, it is expected to increase with both sex ratio and density, and thus provide the thread that ties his results with *G. odontogaster* to my results with *G. buenoi*.

The role of harassment rate will vary with the degree to which females benefit from mating. In cases where females benefit from mating, females should be less reluctant to mate and therefore harassment by males become less important. Although there is no evidence of direct benefits of mating to female water striders (e.g. nutritional, Andersen 1982; Arnqvist 1989b), females of some species may gain an indirect benefit (see above). However, there are a large number of lentic species, such as *G. buenoi*, where neither males nor females appear territorial (e.g. the sub-genus *Gerris*, Arnqvist 1989a; Fairbairn 1990; this study). These species probably gain little or nothing by mating and therefore, harassment of females by amorous males is predicted to play a larger role in their mating systems.

## Conclusion

The mating system of *G. buenoi* can be described as one of convenience polyandry. Females also vary their receptivity in response to increased costly harassment by males and vary mating behaviour in response to other demands. My results suggest that mating conflicts with foraging in *G. buenoi*, and that females adjust receptivity according to these demands. Predation risk may also affect receptivity in water striders (Sih et al. 1990). Further study of the ecological determinants of and trade-offs involved in water strider mating systems will be profitable. The current study demonstrates that females exercise significant control over many of the major components of this mating system. Past research has tended to focus on male interests and control in mating behaviour and has minimized those of females (Walker 1980; Knowlton & Greenwald 1984; Wilcox 1984; Eberhard 1985). Results presented here should encourage researchers to devote more attention to female interests in mating systems.

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