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Pre-copulatory fighting in a water strider: inter-sexual conflict or mate assessment?

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Abstract. In the water strider, *Gerris odontogaster*, the sexes engage in a pre-copulatory struggle. Females are reluctant to mate and try to dislodge males attempting copulation by repeatedly performing backward somersaults. This paper addresses the ultimate significance of the pre-copulatory struggle. (1) Females may be reluctant in order to avoid costly and superfluous copulations (inter-sexual conflict), or (2) females may be assessing the males' quality as mates (mate assessment). In a laboratory experiment the effects of sex ratio and population density on the mating behaviour of *G. odontogaster* were studied. As the density of males increased, females were less reluctant to mate and mated more frequently. The results of the experiment are consistent with predictions generated by a model of a sexual conflict situation, but not with what may be expected if females were assessing the quality of the males. It is concluded that the primary function of female reluctance in this species is simply to avoid copulations. Further, it has been demonstrated in previous studies that females bias matings towards certain male phenotypes, and that the mechanism of selection is female reluctance. The results of this study are discussed in terms of 'good genes' and 'non-adaptive' views of female choice. It is suggested that inter-sexual selection in *G. odontogaster* represents a case of 'non-adaptive' female choice, since mate selection is a side-effect rather than an ultimate aim of female reluctance.

Though sexual reproduction requires contributions from both males and females, inter-sexual conflicts of interests are important in the evolution of many aspects of reproductive behaviour (e.g. Trivers 1972; Parker 1979, 1984). One such aspect in male–female encounters is conflicts over whether or not to mate, where male and female interests often differ (Parker 1979, 1984). Though it is very difficult to make general predictions of the evolutionary outcome of conflicts over the mating decision, such conflicts are thought to resolve towards female interests in most cases (Parker 1979, 1983, 1984; Knowlton & Greenwell 1984; Hammerstein & Parker 1987).

Pre-copulatory interactions between the sexes involve components of aggression in many species, males attempting to overcome female reluctance (Thornhill 1980; Thornhill & Alcock 1983; Hogg 1988; Arnqvist 1989a). In some of these cases, the copulations are thought to be enforced by males against the primary interests of females (see Thornhill 1980). However, these interpretations are often controversial since what appears to be forced copulations by males may actually represent males overcoming mate-assessment behaviour by females, who choose vigorous males as mates (Thornhill 1980). To distinguish forced copulations, one needs to demonstrate (1) that male and female interests in mating are in conflict and (2) that female reluctance represents a general reluctance to mate rather than an adaptive mate-assessment strategy (Thornhill 1980).

Matings in many species of water striders involve aggressive elements; females typically struggle to dislodge males attempting copulation (e.g. Spence 1979; Wilcox 1979; Wheelwright & Wilkinson 1985; Arnqvist 1988, 1989a; Fairbairn 1988; Krupa et al. 1990; Sih et al. 1990). In the water strider *Gerris odontogaster* Zett. matings are initiated by the males, which pounce towards and grasp the females and attempt to achieve copula position and genital contact (Arnqvist 1989a, b). The females are reluctant to mate and try to dislodge the males primarily by repeatedly performed backward somersaults (Arnqvist 1989a). This pre-copulatory struggle may end with either (1) the male being dislodged and the female skating away or (2) female reluctance ceasing after a number of somersaults

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and copulation and subsequent post-copulatory guarding following. During the copulation and post-copulatory guarding the male rides passively on the back of the female.

It has previously been demonstrated that male and female interests in mating are in conflict in *G. odontogaster*. Sperm displacement is typically high in water striders (Arnqvist 1988; Rubenstein 1989), and matings are thus beneficial to males in terms of reproductive success. However, matings are costly to females mainly in terms of increased predation risk, decreased foraging efficiency and increased energetic expenditure, and females do not receive any balancing benefits from multiple matings (Arnqvist 1989b). Females need mate only approximately once every 10th day during their 1–2-month reproductive period in order to receive sufficient sperm to fertilize their eggs (Arnqvist 1989b). Nevertheless, females mate multiply, frequently several times per day (Vepsäläinen 1974; Arnqvist 1989b).

While it is clear that male and female interests are in conflict in *G. odontogaster*, the functional significance of female reluctance and the pre-copulatory struggle is still unknown. The pre-copulatory struggle in *G. odontogaster* may reflect the intersexual conflict of interests in mating, and females may be reluctant simply to avoid costly and superfluous copulations in general (Parker 1979, 1984; Hammerstein & Parker 1987). Matings may then be said to be enforced by males (Thornhill 1980). On the other hand, female reluctance may be a way of assessing the males' endurance, choosing vigorous males with 'good genes' which are able to resist the somersaults as mates. The present study examines the functional significance of female reluctance in *G. odontogaster* by comparing female reluctance at different operational sex ratios and population densities with predictions made from theoretical considerations. Further, some of the consequences of the results in terms of sexual selection are discussed.

THEORETICAL PREDICTIONS

A Model for 'Making the Best of a Bad Job'

How would females behave if they were simply trying to dislodge all males attempting copulation? Wilcox (1984) suggested that since females of the water strider *G. remigis* experience costs during the pre-copulatory struggle, the consequences of being reluctant are not trivial and that female reluctance should be related to male density. However, in order to obtain explicit predictions for the optimal female level of reluctance under different environmental conditions, a simple model is required. The model below considers the various costs of intersexual interactions in *G. odontogaster* (see Arnqvist 1989b), and is essentially a cost-minimizing model where females are assumed to 'make the best of a bad job' in a situation where they are harassed by males. The assumptions are as follows.

(1) The female is previously mated (the spermatheca contains viable sperm).

(2) Females choose an average level of reluctance, that is the maximum number of somersaults a female is prepared to perform (N') before accepting a copulation, and the probability of 'winning' the struggle (dislodging the male) is determined by the level of reluctance the female chooses.

(3) Each somersault during the pre-copulatory struggle involves a certain cost (C') for the female, and a certain probability (pN) of dislodging the male.

(4) A copulation with subsequent guarding involves a certain cost (C_m) for females but no benefits per se.

In this situation a female will, when grasped by a male, struggle to dislodge him. The probability of the female winning a struggle at a specific level of reluctance ($pW_{N'}$) will be

$$pW_{N'} = 1-(1-pN)^{N'} \qquad (1)$$

and the probability of losing ($pL_{N'}$) will be

$$pL_{N'} = (1-pN)^{N'} \qquad (2)$$

Consequently, the probability of dislodgement in the Nth somersault is given by

$$pW_N = (1-pN)^{N-1}pN \qquad (3)$$

The mean probability of dislodging a male in a single somersault (pN) is 0·307 in the laboratory ($N=324$ somersaults, data from experiments in Arnqvist 1989a). The probability distribution of dislodgement produced by the probability density function (3) for $pN=0·3$ and the observed frequency distribution in the laboratory ($N=274$ dislodgements, data from experiments in Arnqvist 1989a) are shown in Fig. 1.

The cost of the struggle for a female will depend on the outcome. If the female loses she will experience N' somersaults, and the struggle cost (C_s) will simply be

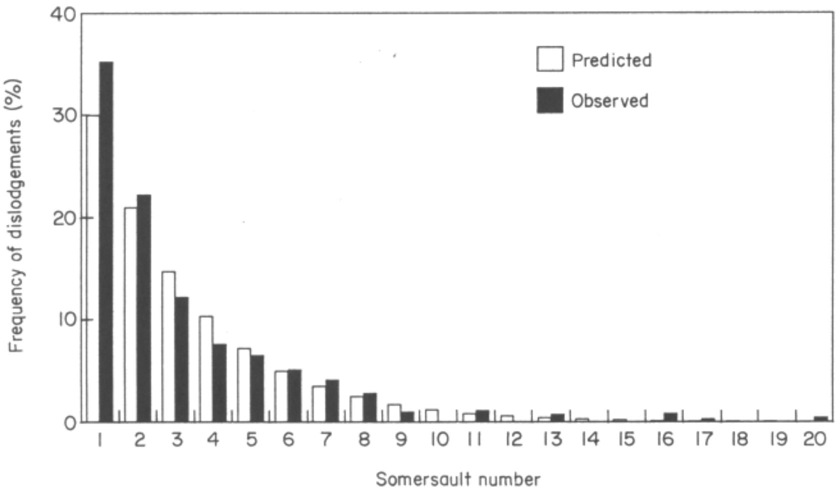

Figure 1. Frequency distribution of dislodgements predicted by the model for $pN=0.3$ compared with observed data ($N=274$).

$$C_s = C'N'$$

If the female wins, however, she will experience an average number of somersaults given by

$$N'' = \frac{\sum_{N=1}^{N'} N(1-pN)^{N-1}pN}{\sum_{N=1}^{N'} (1-pN)^{N-1}pN} \qquad (4)$$

and the average struggle cost (C_s') will be

$$C_s' = C'N''$$

The probability of experiencing C_s or C_s' is determined by the level of reluctance (N') according to equations (1) and (2). If the female loses she will, in addition to the struggle cost C_s, also experience a mating cost C_m. The female's average payoff (P) as a function of the level of reluctance she chooses may then be expressed as

$$P = [1-(1-pN)^{N'}][-C'N''] + [(1-pN)^{N'}][-C'N' - C_m] \qquad (5)$$

Thus, the costs involved in winning or losing are asymmetric, but that is also true for the time during which these costs will be experienced. If the outcome is dislodgement, the female will experience C_s' during the average time she will spend alone (t_a) before being harassed by another male. If the outcome is mating, the female will experience C_s and C_m during the sum of the average time required for a mating (t_m) and t_a. Hence, the final equation may be said to express the female's average payoff per time unit (P')

$$P' = [1-(1-pN)^{N'}][(-C'N'')/t_a] + [(1-pN)^{N'}][(-C'N' - C_m)/(t_a+t_m)] \qquad (6)$$

A female will minimize her costs when equation (6) is maximized.

Natural populations of water striders vary locally with respect to population density and operational sex ratio (Järvinen et al. 1977; Spence 1980; Krupa et al. 1990). These variations will primarily affect the average time females will spend alone after a struggle or a mating (t_a in the above model). Figure 2 shows average female payoff as a function of the level of reluctance (N') for different values of t_a according to equation (6) ($pN=0.3$, other variables arbitrary and constant). The struggle cost (C') and the probability (pN) of dislodging the male are treated as constants in the model. In reality, these parameters are likely to be unstable variables rather than constants (C' increasing and pN decreasing during a specific struggle). However, while treating C' and pN as variables will alter the quantitative output of the model, it will not affect its qualitative predictions (see below). This is also true for the choice of input value of the constants involved in the model.

The Inter-sexual Conflict Hypothesis: Predictions

Two major qualitative conclusions may be made from the model of optimal female reluctance in a

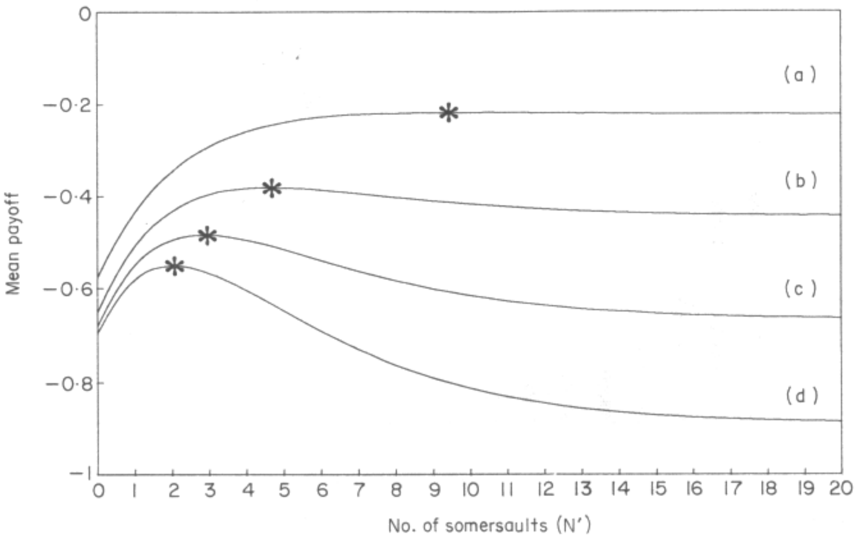

Figure 2. Mean female payoff as a function of the level of reluctance (N') for different times that the female spends alone after a mating (t_a) according to the model of a sexual conflict. Values of t_a are (a) 12, (b) 6, (c) 4 and (d) 3. Optimal levels of reluctance for the different t_a-values are indicated with asterisks. Note that the optimal level of female reluctance decreases as the density of males increases, since t_a is negatively correlated with operational sex ratio and population density. See text for further explanations.

situation of sexual conflict. First, making the best of a bad job for females is to choose an intermediate level of reluctance, representing a trade-off between the costs of the pre-copulatory struggle and mating on one hand, and the 'benefits' (being able to forage alone) on the other. Second, the model predicts that the optimal level of female reluctance increases with an increased t_a (Fig. 2), a variable that is negatively correlated with the numbers of males present (operational sex ratio and/or population density). In other words, when males become more abundant and females are harassed more frequently, females should struggle less intensely. One important consequence of increased male harassment and decreased female reluctance is that females would mate more frequently, even though multiple matings are costly per se (Arnqvist 1989b). Thus, if females alter their level of reluctance in order to minimize their costs and risks, we would expect (1) females to perform fewer somersaults before accepting a male and (2) female mating frequency to increase as population density and the operational sex ratio increases.

The Mate Assessment Hypothesis: Predictions

There have been few attempts to make theoretical predictions of female behaviour in situations where females choose between males with different genetic qualities. Parker (1979, 1983) has developed models where 'optimal selectivity' will depend primarily on the costs of searching for a mate and the relation between offspring fitness and mate selectivity. Further, Janetos (1980) compared several female mate choice strategies in terms of consequences for female fitness. In *G. odontogaster* the level of female preference or choosiness may be quantified as the number of somersaults performed before accepting a male as a mate. Assuming that females are assessing the quality of the males during the pre-copulatory struggle and that females are able to assess the presence of males and alter their level of reluctance accordingly, females should 'set the standard' according to the availability of males (cf. the best-of-*n*-males-strategy of Janetos 1980). In other words, without invoking any specific constraints on female behaviour, females should be more choosy as the number of males (male genotypes) available increases (Janetos 1980). Thus, we would expect (1) *G. odontogaster* females to perform more somersaults before accepting a male as a mate and (2) female mating frequency to be largely unaltered as population density and the operational sex ratio increase.

METHODS

Gerris odontogaster individuals were captured in the Gimonäs pond, south-east of Umeå in northern Sweden (63°48′N, 20°19′E), on 14 May 1990, to be used in a laboratory experiment. The experiment was conducted at 20 ± 1°C, and the illuminated period in the laboratory was adjusted every day to correspond with the daylength in the field.

The water striders used in the experiment were individually marked with enamel paint on their mid- and hindlegs, and introduced into plastic aquaria (0·45 × 0·25 m) in the laboratory on 17 May. Pieces of floating Styrox (5·0 × 10·0 × 0·3 cm) served as resting sites for the water striders. To obtain independent measures of the relative effects of the operational sex ratio and population density on the mating behaviour of the water striders, I used a 2 × 3 factorial design. Levels of density were (1) six individuals per aquarium and (2) 12 individuals per aquarium. Levels of operational sex ratio (defined as the number of males/total number of individuals) were 0·33, 0·50 and 0·66. Four replicate aquaria of each treatment were studied. All water striders were fed daily with three frozen *Drosophila* fruitflies per individual.

I studied the water striders in the experimental aquaria for 9 h (0800–1700 hours) every day during 10 consecutive days (21–30 May). Each aquarium was studied every half-hour, and all matings were recorded. Since all water striders were individually marked, the mating history of each individual could be followed allowing an estimate of individual mating frequency as well as the duration of each mating (males have a refractory period of approximately 2 h). Additionally, for all observed mating attempts that led to copulation, I recorded the number of somersaults that the female performed prior to copulation. Aquaria were considered as the experimental unit in this study, and the mean values from each aquarium were thus used for statistical analysis.

RESULTS

The mating behaviour of *G. odontogaster* was profoundly affected by both the operational sex ratio and population density. The level of female reluctance, quantified as the mean number of female somersaults performed prior to copulation in successful male mating attempts, was significantly reduced by increases in both operational sex ratio and density (Fig. 3, Table I). There was no statistical interaction between the two factors.

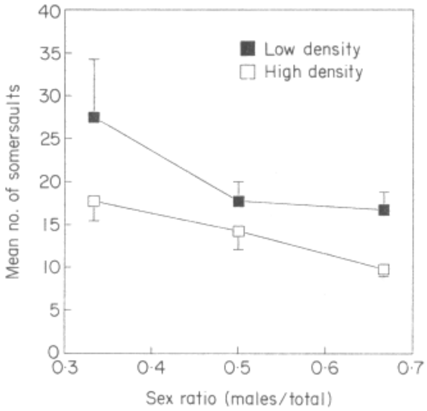

Figure 3. Mean level of female reluctance, measured as the number of somersaults prior to copulation in successful male mating attempts, in each treatment combination of the operational sex ratio and population density manipulation experiment (see Table I). Error bars represent one standard error.

Table I. Two-way ANOVA of level of female reluctance, measured as the mean number of somersaults in successful male mating attempts

Source	*df*	Mean square	*F*	*P*
Sex ratio	2	185·79	4·229	0·031
Density	1	273·37	6·223	0·023
Sex ratio × density	2	19·62	0·447	0·647
Residual	18	43·93		

See also Fig. 3.

The operational sex ratio had a significant effect on female mating frequency (Fig. 4), females mating more frequently in male-biased situations, whereas density showed no significant effect (Table II). Male mating frequency on the other hand, was not significantly affected by either operational sex ratio or density (Fig. 5, Table III). Further, mating duration increased with both increasing density and operational sex ratio (Fig. 6, Table IV).

To summarize the results, as the density of males increased females struggled less intensely during the pre-copulatory fight before accepting a male as a mate and consequently mated more often, and the average mating duration increased.

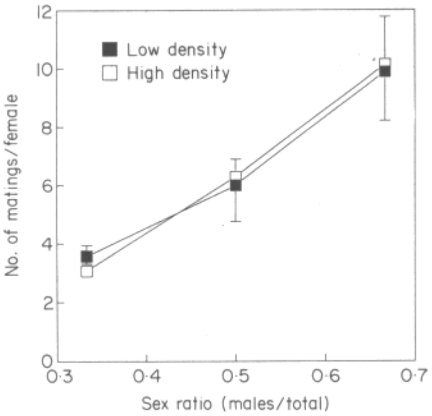

Figure 4. Female mating frequency, estimated as the mean number of observed matings per female during the experiment, in each of the treatment combinations (see Table II). Error bars represent one standard error.

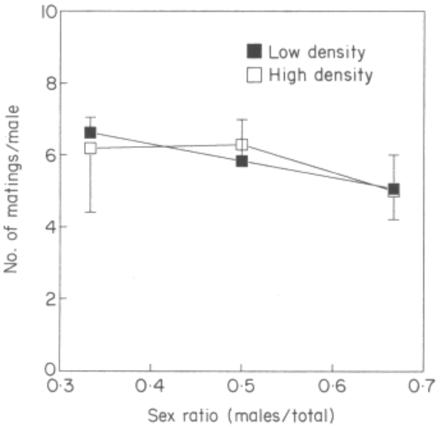

Figure 5. Male mating frequency, estimated as the mean number of observed matings per male during the experiment, in each of the treatment combinations (see Table III). Error bars represent one standard error.

Table II. Two-way ANOVA of female mating frequency, estimated as the mean number of observed matings per female during the experiment

Source	*df*	Mean square	*F*	*P*
Sex ratio	2	90·171	16·46	<0·001
Density	1	0·001	0·00	0·989
Sex ratio × density	2	0·400	0·07	0·930
Residual	18	5·478		

See also Fig. 4.

Table III. Two-way ANOVA of male mating frequency, estimated as the mean number of observed matings per male during the experiment

Source	*df*	Mean square	*F*	*P*
Sex ratio	2	4·099	0·937	0·410
Density	1	0·001	0·000	0·987
Sex ratio × density	2	0·404	0·092	0·912
Residual	18	4·376		

See also Fig. 5.

DISCUSSION

The Model

Resolutions of evolutionary games of inter-sexual conflicts over the mating decision are typically very complex (Parker 1979, 1983, 1984; Knowlton & Greenwell 1984; Hammerstein & Parker 1987). However, the cost-minimizing model of a sexual conflict situation presented in this study deals with female decision rules during the pre-copulatory struggle, rather than predicting a resolution of an evolutionary game. Males are assumed to have won the evolutionary conflict over the mating decision in the sense that females are forced to exercise energetically expensive and risky behaviour in order to reject males attempting copulation. This may be because (1) water striders inhabit strictly two-dimensional habitats where active females cannot avoid males and (2) males have evolved a grasping apparatus making it more difficult for females to reject them (Arnqvist 1989a; Krupa et al. 1990). In this situation, females are assumed to make the best of a bad job (cf. Parker 1979, page 133).

Previous results support the assumptions of the model of a sexual conflict in *G. odontogaster*; females mate multiply and bear higher costs and receive less benefits in mating than do males (see Arnqvist 1989b). Further, since both costs and benefits involved in pre-copulatory interactions and matings are asymmetrical in favour of males (Arnqvist 1989b), males should theoretically never give in first (withdraw) in a conflict over matings (Hammerstein & Parker 1987). Observations of the pre-copulatory struggle support this conclusion.

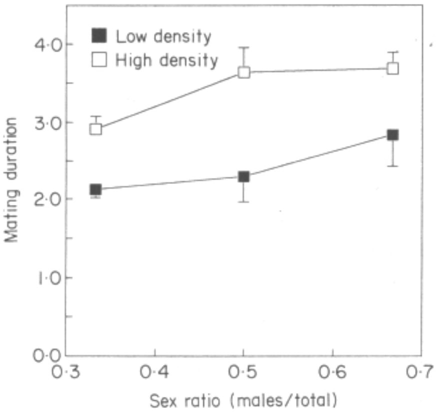

Figure 6. Mating duration, measured as the average number of 30-min intervals per mating, in each of the treatment combinations (see Table IV). Error bars represent one standard error.

Table IV. Two-way ANOVA of mating duration, estimated as the average number of recorded 30-min intervals per mating

Source	*df*	Mean square	*F*	*P*
Sex ratio	2	1·122	3·735	0·044
Density	1	5·930	19·739	<0·001
Sex ratio × density	2	0·187	0·621	0·549
Residual	18	0·300		

See also Fig. 6.

Males seem always to choose a higher persistence time than do females. The outcome of the pre-copulatory struggle is therefore best described as a female optimization rather than a frequency-dependent ESS (cf. Parker 1979, 1984).

Inter-sexual Conflict or Mate Assessment?

The model of a sexual conflict over the mating decision suggested that females should struggle less intensely before accepting a male as a mate, and consequently mate more frequently, when the density of males is high. The observed changes in female mating behaviour with operational sex ratio/density correspond well with these predictions, while the predictions from a mate assessment perspective were not supported. Hence, all available information suggests that the primary function of female reluctance in *G. odontogaster* is simply to avoid costly and superfluous copulations, rather than to choose the most vigorous mates. Still, it could be argued that the females are assessing mate quality within certain constraints (e.g. energetic) dictated by factors related to the sex ratio (Janetos 1980; Parker 1983). However, such arguments need not, as the model demonstrates, be invoked to explain fully the existence of and variations in female reluctance in *G. odontogaster*. In agreement with this conclusion, Parker (1984) argued that female mating patterns are more likely to be formed by environmental pressures, such as time or energy waste, than by factors related to the genetic quality of the potential mates.

Since there is an intense basic inter-sexual conflict over matings in *G. odontogaster* (Arnqvist 1989b), and since females struggle to avoid matings in general, successful copulations may be said to be forced by males in the sense that females are forced to accept matings that are costly and superfluous per se. Similar scenarios may be present in several other water striders as well, since pre-copulatory and copulatory interactions in these species closely resemble those of *G. odontogaster* (e.g. Spence 1979; Wilcox 1979; Wheelwright & Wilkinson 1985; Arnqvist 1988; Fairbairn 1988; Krupa et al. 1990; Sih et al. 1990). Thornhill (1980) has argued that forced copulations should occur mainly in species in which males provide females with important resources. However, this is clearly not the case in *G. odontogaster* (Arnqvist 1989b).

In addition to the inter-sexual conflict over whether or not to mate, the duration of the copulatory guarding phase should often constitute another conflict in water striders. While males benefit from copulatory guarding (Arnqvist 1988; Rubenstein 1989), females suffer from carrying passive males on their backs (Arnqvist 1989b; Krupa et al. 1990). Females typically terminate matings by dislodging the male, and if females are generally less reluctant in mating when the density of males is high (by analogy with the pre-copulatory interactions), we would expect mating duration to increase with male density in water striders. Available data seem to support this prediction. Clark (1988) demonstrated that copulation duration was highest under male-biased sex ratios in *G. remigis*, and in this study the mating duration of *G. odontogaster* increased with both operational sex ratio and density. In agreement with this, Wilcox (1984) found that when the rate of harassment by males attempting copulation was high, a

G. remigis female could forage effectively only when carrying a passive male on her back and should thus not resist copulatory guardings. As indicated in the model presented in this paper, variations in a number of factors other than sex ratio and density should also affect cost–benefit trade-offs concerning the mating behaviour in water striders. For example, Sih et al. (1990) found that the mating behaviour of *G. remigis* is affected by predation risk and food availability.

The two fundamentally different views of female reluctance in *G. odontogaster* discussed in this paper correspond in several ways to a current controversy regarding sexual selection by female choice. Sexual selection by female choice involves two components: a male trait and a female mating preference for this trait (e.g. Darwin 1871; Majerus 1986; Kirkpatrick 1987a). The mating preference may be due to any mechanism by which females tend to bias matings towards certain male phenotypes (Kirkpatrick 1987a). The current view of sexual selection by female choice may be divided into two major schools (Bradbury & Andersson 1987; Kirkpatrick 1987a). The 'good genes' school postulates that female preferences evolve under selection for females to mate with ecologically adaptive male genotypes. In contrast, the 'non-adaptive' school holds that preferences evolve for other reasons, and that selection will often cause males to evolve maladaptively with respect to their ecological environment. *Gerris odontogaster* is a sexually dimorphic species, males having a grasping apparatus consisting of two ventral abdominal processes, which is essential for males to succeed in forced copulations. Furthermore, the length of the processes is heritable and males with long abdominal processes have a greater ability to endure female reluctance than males with short abdominal processes (Arnqvist 1989a). Owing to their reluctance, females bias matings towards males with long abdominal processes (Arnqvist 1989a). The trait may thus be said to be subjected to sexual selection by female choice (sensu Kirkpatrick 1987a). Kirkpatrick (1987a, b) emphasized that information about the male trait only is insufficient to resolve the controversy over female choice, and that more effort should be made to understand the mechanism and evolution of the female preference (see also Sullivan 1989). Since female reluctance is the mechanism of selection in *G. odontogaster*, one may ask whether it represents an adaptation for choosing vigorous males with good genes as mates or if the bias in matings is merely a side-effect of, in this case, a sexual conflict? As concluded above, females struggle to avoid costly matings in general rather than to assess the mate's genetic quality, suggesting that female mating preferences for certain male genotypes (Arnqvist 1989a) is a by-product of evolutionary forces unrelated to intraspecific mate discrimination. Sexual selection by female choice in *G. odontogaster* thus seems to be a side-effect rather than the ultimate cause of the reluctance, and would hence represent a case of 'non-adaptive' female choice (Kirkpatrick 1987a, b).

One remarkable implication of the results in this study is that the intensity of sexual selection (Wade & Arnold 1980; Wade 1987) should be negatively correlated with the operational sex ratio. This is contrary to what is commonly observed and assumed (Arak 1983; Thornhill & Alcock 1983; Verrell 1983; Sutherland 1987), and results from females being less reluctant to mate (and thus less discriminatory) when male density is high. Variations in sex ratios (and population densities) within and among populations of *G. odontogaster* should thus reflect variations in the intensity of sexual selection (see Arnqvist 1991). Such differences in selective regimes may be of great importance in maintaining additive genetic variance in male traits (Hedrick 1986), and should be given attention in future studies.

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