The effects of operational sex ratio on the relative mating success of extreme male phenotypes in the water strider *Gerris odontogaster* (Zett.) (Heteroptera; Gerridae)

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In evolutionary theory, the concept of operational sex ratio is important since it relates to the intensity of sexual selection. The more the operational sex ratio is biased towards males, the higher is the expected variance in reproductive success among males (Emlen & Oring 1977; Wade & Arnold 1980) which corresponds to a greater potential for sexual selection (Wade & Arnold 1980; Sutherland 1987; Wade 1987). Empirical studies have demonstrated that male behaviour may change with the degree of competition for females (e.g. Arak 1983; Verrell 1983; Lawrence 1986; Clark 1988), and that the variance in male mating success may covary with the operational sex ratio (Thornhill & Alcock 1983).

In the water strider, *Gerris odontogaster*, the sexes engage in a precopulatory struggle; females are reluctant to mate and try to dislodge mounting males (Arnqvist 1989a, b). Males are provided with two abdominal processes, which enable them to grasp females during mating (Arnqvist 1989a). Males with longer processes have a higher ability to endure female reluctance than males with shorter processes, and because of this asymmetry, matings are biased towards males with long processes (Arnqvist 1989a). I have elsewhere (Arnqvist 1992) predicted that (in contrast to the general theory) the intensity of sexual selection in male *G. odontogaster* should be negatively correlated with the operational sex ratio. This reversal of the predicted relation between sex ratio and intensity of sexual selection should arise as a result of females altering their behaviour as the operational sex ratio changes; female *G. odontogaster* are less reluctant to mate and thus less discriminatory when the operational sex ratio is male biased (Arnqvist 1992). Thus, the relative importance of long abdominal processes should be negatively correlated with the sex ratio. This study provides an

empirical test of the relation between the intensity of selection and sex ratio in *G. odontogaster*.

Unmated individuals of *G. odontogaster* were sampled on 8–9 May 1989 in the Gimonäs pond, south-east of Umeå, northern Sweden (63°48′N, 20°19′E). Males ($N = 704$) were anaesthetized and the length of the abdominal processes was measured with a micrometer eyepiece. The mean length ($\pm$ SE) of the processes was 0·162 ($\pm 0·001$) mm. Two groups of male phenotypes with extreme secondary sexual characteristics (short processes ($\leqslant 0·14$ mm) and long processes ($\geqslant 0·20$ mm)) were selected for a field enclosure experiment.

All individuals were marked with enamel paint on the pronotum so I could distinguish between males with long processes, males with short processes and females in the field. The water striders were introduced on 25 May into floating enclosures in the field. The enclosures ($N = 15$) measured $1·0 \times 1·0 \times 0·3$ m (area $1·0$ m²) and consisted of aluminium frames provided with Styrox floating elements. Twenty water striders were placed in each of the enclosures, and the operational sex ratio was varied between enclosures to produce a gradient ranging from 0·2 to 0·8 (males/total). In all enclosures 50% of the introduced males were males with long processes and 50% were males with short processes, while females were chosen at random.

The enclosures were visited twice every day from 26 May to 9 June. To estimate the relative mating success of the two male groups, I recorded the number of mating pairs in each enclosure and the type of each mating male (short or long abdominal processes) at each visit.

Since the estimates of relative mating success could be biased if the mating duration differed between the two groups of males, I performed a laboratory experiment to examine whether such a difference exists. Into each of a number of plastic
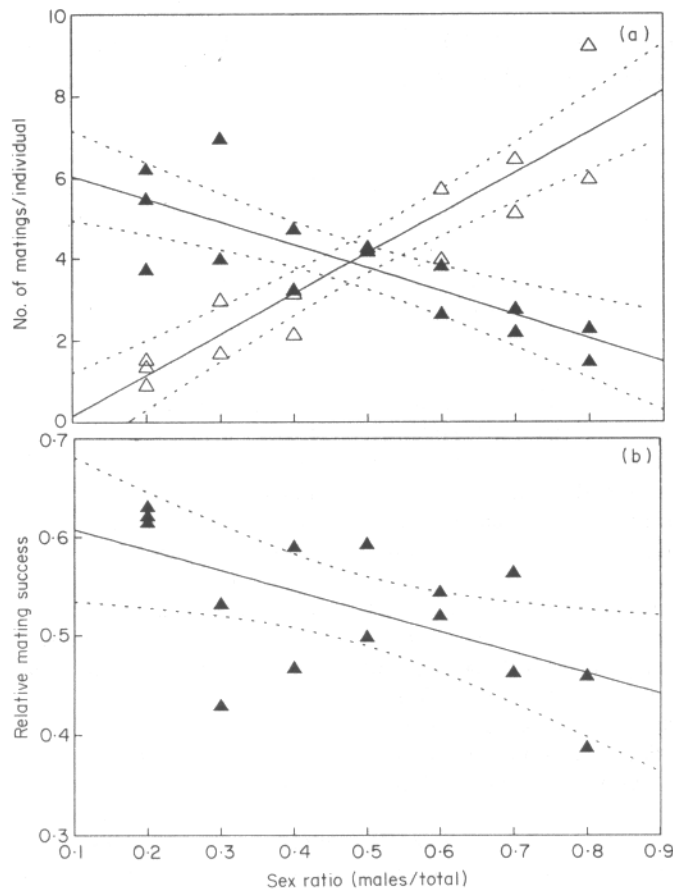
Figure 1. (a) The mean number of observed matings per individual during a 14-day period in enclosures with different operational sex ratios ($r = 0.926$, $P < 0.001$ for females ($\triangle$), and $r = -0.800$, $P < 0.001$ for males ($\blacktriangle$)), and (b) the relative mating success of males with long abdominal processes (number of matings of males with long processes/total number of observed matings) for different operational sex ratios ($r = -0.574$, $P < 0.02$). Dashed lines represent 95% confidence limits of regression lines.

aquaria (0.45×0.25 m, $N = 15$), one male with long processes and one male with short processes were introduced with two females. The water striders were fed daily with three fruitflies per individual. The aquaria were studied for 9 h during 3 consecutive days, starting 4 days after the introduction into the aquaria. During the experiment I recorded the duration of all observed matings. The mean value of mating duration for each male was used in subsequent statistical analysis.

In the laboratory experiment, there was no significant difference in mating duration between males with long and short processes (Mann–Whitney U-test, $P > 0.1$), suggesting that the estimates of relative mating success in the field experiment

are unbiased. The average ($\pm$SD) mating duration (pooled data) was 54.8 ± 24.1 min ($N = 30$).

The mean number of observed matings per individual in the field experiment was positively correlated with the sex ratio for females and negatively correlated with the sex ratio for males (Fig. 1a). The relative mating success of males with long processes, estimated as the number of matings of males with long abdominal processes divided by the total number of matings, was negatively correlated with the sex ratio (Fig 1b). Thus, males with long processes had a relatively greater ability to acquire mates in female-biased situations.

In the laboratory female *G. odontogaster* become less reluctant during the pre-copulatory struggle and

female mating frequency increases when the sex ratio increases (Arnqvist 1992). The positive relationship between the number of observed matings per females and the sex ratio found in this experiment implies that this is the case also in the field (see Arnqvist 1989b, 1992, for discussion of sexual conflicts). If female reluctance decreases with increasing sex ratio we would expect the importance of long abdominal processes in acquiring matings to be related to the sex ratio. Indeed, the relative mating success of males with long abdominal processes decreased with increasing sex ratio. Though relative mating success of males with long processes is not a direct measure of the intensity of sexual selection (Wade 1987), it is a result of an underlying variance in mating success related to process length, so that the larger the variance in mating success between the phenotypic groups the larger the relative mating success becomes. Thus, we may conclude that the relative mating success, as an estimator of the intensity of sexual selection for long abdominal processes, was negatively correlated with the sex ratio. This is, as mentioned above, contrary to what is generally found. The results of this study stress the need of a thorough understanding of the mechanisms of selection before predicting variations in the intensity of selection. The relation between the sex ratio and the intensity of sexual selection (or the potential for sexual selection; see Wade 1987) may not be as straightforward as is commonly believed, since it may be influenced not only by changes in male behaviour (cf. Lawrence 1986, 1987) but also by changes in female behaviour related to variations in the sex ratio.

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