

# Antagonistic pre- and post-copulatory sexual selection on male body size in a water strider (*Gerris lacustris*)

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A crucial question in sexual selection theory is whether post-copulatory sexual selection reinforces or counteracts conventional pre-copulatory sexual selection. Male body size is one of the traits most generally favoured by pre-copulatory sexual selection; and recent studies of sperm competition often suggest that large male size is also favoured by post-copulatory sexual selection. In contrast to this general pattern, this study shows that pre- and post-copulatory sexual selection act antagonistically on male body size in *Gerris lacustris*. One large and one small male were kept together with two females in this experiment. Large males had a significant mating advantage, but small males copulated longer and gained higher fertilization success from each mating. Large and small males, however, gained similar reproductive success, and there was no overall correlation between mating success and reproductive success. These results suggest that estimates of male fitness based solely on mating success should be viewed with caution, because of potentially counteracting post-copulatory selection.

**Keywords:** sexual selection; male body size; sperm competition; mating success; fertilization success

## 1. INTRODUCTION

Sexual selection according to Darwin (1871) is the difference in reproductive success caused by competition over mates, either through male–male competition or female-choice mechanisms. In most studies of sexual selection, male mating success has been used as a measure of male reproductive success, which may be appropriate in some cases (e.g. Pemberton *et al.* 1992; Abell 1997). However, competition for fertilizations continues inside the female through sperm competition (Parker 1970) and/or cryptic female choice (Eberhard 1996). Thus, a male's reproductive success is the product of the number of females he mates with and the number of ova he fertilizes per female. Estimates of purely mating success may be poor estimates of actual male reproductive success (Hughes 1998). Modern sexual selection thinking is inevitably bound to include both pre- and post-copulatory processes.

One would expect male traits of importance for both pre- and post-copulatory processes to evolve. In numerous case-studies and reviews, male body size has been identified as a trait commonly favoured by pre-copulatory sexual selection (e.g. Andersson 1994). Recent studies of intraspecific variation in fertilization success suggest that large male size is similarly favoured by post-copulatory sexual selection (Birkhead & Møller 1998). In several species where large males have a mating advantage, it has been shown that large body size also correlates with high relative fertilization success (Otronen 1984, 1994; McLain 1985, 1991; Simmons 1988; Lewis & Austad 1990, 1994; Simmons & Parker 1992; LaMunyon & Eisner 1993; Parker & Simmons 1994). Post-copulatory sexual selection may thus act to reinforce the potential reproductive rate and increase the strength of sexual selection on male body size (Møller 1998). There are, however, studies showing that large body size is advantageous in competition over mates in one respect,

but disadvantageous in others, i.e. there is antagonistic pre-copulatory sexual selection on body size (e.g. Searcy 1979; Deinert *et al.* 1994; Neems *et al.* 1998). Also pre- and post-copulatory sexual selection may have counteracting effects on male body size. Earlier work suggests a possible trade-off between number of matings by a male and number of sperm allocated to each female (Pitnick 1991; Simmons 1995; Warner *et al.* 1995).

In the genus *Gerris*, females mate multiply and store sperm for several weeks (Arnqvist 1997). Male mating behaviour is characterized by scramble competition with post-copulatory mate guarding (Arnqvist 1997). The mating is initiated by male coercion without prior courtship. During the copulation and guarding the male rides on the back of the female, which is costly for the female, and females are generally reluctant to mate (Arnqvist 1997). Female resistance puts males under directional pre-copulatory sexual selection for increased body size in order to better subdue females (e.g. Sih & Krupa 1992; Fairbairn & Preziosi 1996). However, small males have been found to copulate longer than large males (Rowe & Arnqvist 1996). This might enhance their relative fertilization success and could thus allow small males to compensate for the lower mating success. In this study, I simultaneously examined pre- and post-copulatory sexual selection on male body size in the water strider *Gerris lacustris*, by letting one large and one small male compete over matings and fertilizations.

## 2. MATERIAL AND METHODS

### (a) *Collection and rearing conditions*

Males and females of the water strider *G. lacustris* were collected in a pre-reproductive state at emergence from diapause in early spring 1999 near Göteborg, Sweden. The water striders were brought into a laboratory with a temperature of 20–22 °C, and a light regime simulating natural conditions. These laboratory conditions were maintained throughout the experiment. In

the laboratory, females were kept isolated from males in aerated pools (diameter, 0.8 m; water depth, 7 cm). Female virginity was checked before the experiment by collecting eggs from isolated females over a minimum of eight days. Eggs laid during isolation were checked for embryonic development and all females that laid any fertilized eggs were discarded.

Males were initially kept in aerated pools with diameter of 1.8 m. Each male was scored for body size (distance from the anterior margin of the eye to the most posterior medial point of the seventh abdominal segment, ventral view) using an ocular micrometer in a dissecting microscope ( $\times 6.4$ ). Male body size was on average 7.7 mm (s.d. = 0.30 mm,  $n = 628$ ). The extreme 25 percentiles of the size distribution were used as experimental males (small, 6.6–7.6; large, 7.9–8.4 mm). Large and small males were kept in separate aerated plastic pools (diameter, 1.2 m; water depth, 7 cm) together with non-experimental females.

All water striders were fed frozen early instar *Gryllus* crickets, and Styrofoam™ pieces were provided as resting sites. Typewriter correction fluid was used to mark the water striders individually.

### (b) *Relative fertilization success*

Fertilization success was estimated by the sterile-male technique (Parker 1970). Randomly chosen males were sterilized by exposure to high-energy X-rays. Males were irradiated the day before the experiment using a linear electron accelerator, emitting 6 MV photon beams. The absorbed dose was 130 Gy at a dose rate of about 10 Gy min<sup>-1</sup>. Irradiated males were assumed to have functional sperm with lethal mutations that prevent normal embryonic development. The proportion of viable eggs laid by a female mated sequentially with one normal (N) and one irradiated (R) male was used as an estimate of the relative fertilization success of the normal male.

### (c) *Experimental matings*

To investigate how body size affects mating and fertilization success, one male from each size category, one normal and one irradiated, was allowed to compete for fertilization of the ova from two females. All males were mated once, four days before the experiment, with a non-experimental female, and the males were thereafter individually isolated. The common mating history was assumed to produce similar levels of sperm stores. In the morning of day 1 of the experiment, two randomly chosen virgin females were placed together with one small and one large male in a plastic jar (diameter, 27 cm; water depth, 3.5 cm) with eight pieces of balsa wood (2 cm  $\times$  1 cm) as egg-laying substrate. One hundred replicates were set up over a period of about two weeks. I used a balanced design, with a large irradiated male in half of the replicates and a small irradiated male in the other half.

The two females and the two males were kept together for two days and mating behaviours were sampled at 10 min intervals during four 4 h periods (morning and afternoon each day). Mating status was classified as single, copulating (genital contact) or guarding (no genital contact), and the mating partner was identified. Before each observation period, all remaining food was removed and mating pairs were separated. Some very short matings may have passed undetected between the spot checks. Earlier experiments, however, suggest that although short matings occur, they are infrequent (Rowe & Arnqvist 1996; I. Danielsson, unpublished data). Males were removed after the last observation on the second day, and females were left in the jars.

The balsa pieces with the eggs were collected on day 5, and the females were moved to a smaller jar (17 cm  $\times$  17 cm  $\times$  10 cm, water depth 3 cm) with four new pieces of balsa wood. Eggs were collected again on day 9. After collection, the eggs were allowed to mature for eight days in small plastic cups with water. The eggs were then counted and classified as viable or non-viable. Normally developed eggs were brownish at this time with distinct red eyespots. Opaque and yellowish eggs were scored as non-viable. The proportion of viable eggs laid by the females during the nine days was used to estimate relative fertilization success of each male.

Control matings were performed to check the effect of the irradiation treatment. The probability of viable eggs arising from matings with irradiated males was estimated from matings with two irradiated males (RR matings,  $n = 16$ ). Similarly, the probability of non-viable eggs arising from matings with normal males was estimated from control matings with two normal males (NN matings,  $n = 15$ ).

### (d) *Statistical analyses*

Proportional response data were analysed with generalized linear models (GLIM) using binomial errors and a logit link function (Crawley 1993). The sample size was used as the binomial denominator (Crawley 1993). I used the log-likelihood ratio (LLR) to assess the goodness of fit of the model to the data. The change in LLR when adding factors to a reduced model is asymptotically  $\chi^2$ -distributed. William's correction procedure for overdispersed data was used (Crawley 1993). Other statistical analyses were performed with procedures in SAS. All tests were two-tailed and means  $\pm$  s.d. are given unless otherwise stated.

## 3. RESULTS

The proportion of viable eggs laid by females involved in NN and RR matings was  $0.90 \pm 0.14$  and  $0.27 \pm 0.18$ , respectively. Irradiation thus had a significant effect on the viability rate (GLIM,  $\chi^2 = 26.6$ , d.f. = 1,  $p < 0.001$ ). However, due to incomplete sterilization of irradiated males and possibly reduced competitive ability of irradiated sperm, the relative total fertilization success was skewed towards the normal male in competing pairs of males (table 1). Thus, the proportion of viable eggs overestimates the true relative fertilization success of normal males. The proportion of viable eggs, however, represents a relative measure of the fertilization success of normal males. To avoid any problems with different competitive ability of R and N sperm, I restricted my analyses to the variation in mating behaviour and relative fertilization success within normal males.

Large males copulated more frequently than small males (see table 1 for statistical evaluations). Small males, however, gained higher relative fertilization success per copulation. There was a significant negative correlation between relative mating success and relative fertilization success per copulation (Spearman's  $r_s = -0.518$ ,  $n = 100$ ,  $p < 0.001$ , figure 1), which further indicates antagonism between pre- and post-copulatory sexual selection. This correlation should be interpreted with caution, however, because of potential problems with autocorrelation. Relative reproductive success did not differ significantly between small and large males. There was no correlation between relative mating

Table 1. *Mating and fertilization characteristics of small and large normal males (means  $\pm$  s.d.)*(Differences between large and small males were tested by Wilcoxon rank sum test ( $z$ -statistic) or using generalized linear models ( $\chi^2$ -statistic).)

dependent variable	large male	small male	statistic	$p$
relative mating success (proportion of copulations by normal male)	0.546 $\pm$ 0.066	0.468 $\pm$ 0.078	$\chi^2 = 24.4$ d.f. = 1	< 0.001
relative fertilization success per copulation (proportion of viable eggs per copulation)	0.041 $\pm$ 0.017	0.049 $\pm$ 0.020	$z = -1.99$ $n_1 = n_2 = 50$	0.047
relative reproductive success (proportion of viable eggs)	0.795 $\pm$ 0.215	0.816 $\pm$ 0.220	$\chi^2 = 0.25$ d.f. = 1	0.62
copulation duration (min)	17.7 $\pm$ 2.9	24.1 $\pm$ 7.1	$z = -5.78$ $n_1 = n_2 = 50$	< 0.001
guarding duration (min)	27.2 $\pm$ 13.8	30.4 $\pm$ 18.6	$z = -0.66$ $n_1 = 49, n_2 = 50$	0.51
proportion of matings with guarding	0.501 $\pm$ 0.211	0.497 $\pm$ 0.199	$\chi^2 = 0.003$ d.f. = 1	0.96
mating interval (min)	30.7 $\pm$ 11.6	33.0 $\pm$ 11.0	$z = -1.48$ $n_1 = n_2 = 50$	0.14

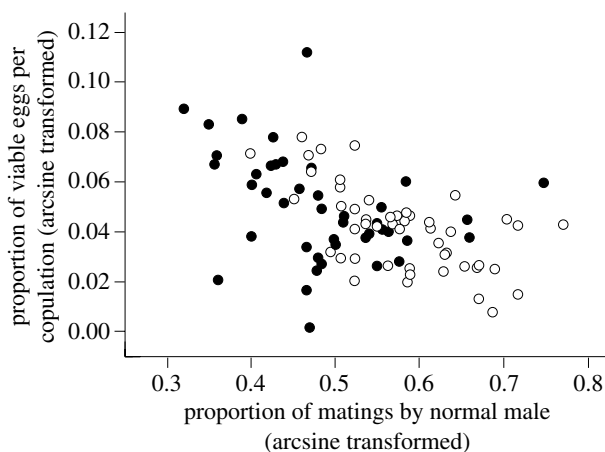


Figure 1. The relationship between relative mating success (proportion of matings by normal male) and relative fertilization success per copulation (proportion of viable eggs per copulation). Closed symbols, small males; open symbols, large males.

success and relative reproductive success (Spearman's  $r_s = -0.151$ ,  $n = 100$ ,  $p = 0.13$ , figure 2).

One possible reason for the higher relative fertilization success per mating of small males is that they gained fertilizations at a faster rate while copulating. However, fertilization success per unit time in copula did not differ between the two groups (Wilcoxon rank sum test,  $z = 1.13$ ,  $n_1 = n_2 = 50$ ,  $p = 0.26$ ). Small males, however, had longer mean copulation duration than large males (table 1). Small males also tended to accumulate more time in copula than large males (Wilcoxon rank sum test,  $z = -1.84$ ,  $n_1 = n_2 = 50$ ,  $p = 0.066$ ).

Mean time between matings (time between the end of a copulation and the beginning of another) was  $31.8 \pm 11.3$  min. Despite differences in mating frequency, I did not find any significant difference in mating interval between large and small males (table 1). Time between matings increased during the experiment for 83 males ( $b > 0$ ) and decreased for the remaining 17 males ( $b < 0$ ), and the regression coefficient was larger than zero more

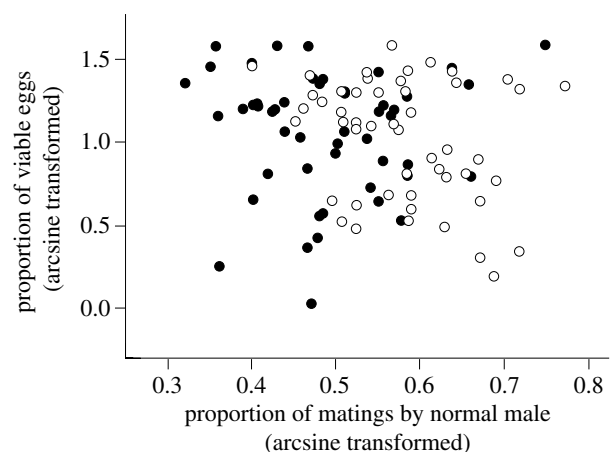


Figure 2. The relationship between relative mating success (proportion of matings by normal male) and relative reproductive success (proportion of viable eggs). Closed symbols, small males; open symbols, large males.

often than expected by chance for both large and small males (sign test, small males,  $n = 50$ ,  $p < 0.001$ ; large males,  $n = 50$ ,  $p < 0.001$ ). In contrast, copulation duration decreased during the experiment for 87 males ( $b < 0$ ), increased for 11 males ( $b > 0$ ) and remained unchanged for two males ( $b = 0$ ). The regression coefficient was less than zero more often than expected by chance for both large and small males (sign test, small males,  $n = 48$ ,  $p < 0.001$ ; large males,  $n = 50$ ,  $p < 0.001$ ).

There was no difference in guarding duration, nor in frequency of guarding between large and small males (table 1). It should be noted that in *G. lacustris* males guard very briefly, mostly less than 1 min (Danielsson & Askenmo 1999) and some short guardings probably went undetected in this study.

#### 4. DISCUSSION

##### (a) *Antagonistic sexual selection*

Conventional wisdom is that sexual selection favours large males, usually via improved competitive ability in

male–male conflicts (Andersson 1994). Some form of counteracting natural selection is often assumed to balance the sexual selection for large body size, but this study instead suggests antagonistic sexual selection on male body size. Large males gained higher mating success, but small males were compensated by higher fertilization success in each mating. The fact that sexual selection can be self-limiting has seldom been emphasized. In the red-winged blackbird, however, large body size was advantageous in male contests for territories, but large males suffered from energy limitations, and had less time for territory defence and display activities (Searcy 1979). Another example of antagonistic pre-copulatory sexual selection on male body size was found in the midge *Chironomus plumosus*, where small males had a mating advantage in swarms, but large males remained longer in the swarm each evening (Neems *et al.* 1998). In the moth *Plodia interpunctella*, there was an investment trade-off between traits for mate searching and sperm production (Gage 1995). A large thorax improved mating success, but reduced fertilization success indirectly, since a large thorax reduced investment in testes. In water striders, antagonistic pre- and post-copulatory sexual selection seems to arise from a trade-off between mating frequency and number of sperm transferred in each mating.

#### (b) *Male allocation strategies*

A recent experiment suggests that water strider males are constrained by sperm production, and need some time to replenish sperm stores after mating with a female. Male *G. lateralis* with a short recovery period (2 h) performed shorter copulations and transferred less sperm than did males with a long recovery period (48 h) (Arnqvist & Danielsson 1999). The average recovery period in the current experiment was 32 min, and males probably remated before their sperm stores were fully replenished. Furthermore, copulation duration decreased and mating interval increased during the experiment, as expected in the case of sperm depletion. This result is corroborated by the observation that sperm is expensive and time-consuming to produce in several insect species (e.g. Dewsbury 1982; Eady 1995; Bissoondath & Wiklund 1996). Since sperm replenishment rate apparently is independent of body size in *Gerris* males (Arnqvist & Danielsson 1999), large males allocating sperm among more mates due to higher mating frequency, would transfer less sperm than small males to each female. An earlier experiment showed that copulation duration in *G. lateralis* correlated with the male's ejaculate size and relative fertilization success (Arnqvist & Danielsson 1999). In the present study, small males stayed longer in copula than large males, suggesting that small males transfer more sperm per mating, thereby gaining higher relative fertilization success. Thus, large body size seems to indirectly limit a male's relative fertilization success because of more frequent matings (c.f. Pitnick 1991; Warner *et al.* 1995). Although no significant difference in reproductive success was found, large males may gain higher total fitness in the end, for instance due to benefits from partitioning sperm among many females (Pitnick & Markow 1994).

Another possible reason for shorter copulations by large males is that they can acquire a new mate faster than small males. Optimality theory, assuming dimin-

ishing returns while in copula, then predicts large males to interrupt copulations earlier (Parker 1998). Large males would gain higher reproductive success by this strategy. My results do not corroborate such an explanation, since reproductive success was similar for small and large males. One would also expect shorter copulations if large males transfer sperm at a faster rate and due to this have a more steep fitness return function (Simmons & Parker 1992). However, I did not find any difference between small and large males in fertilization rate per unit time in copula. Neither did sperm transfer rate correlate with body size in *G. lateralis* (Arnqvist & Danielsson 1999). The results of this study do not exclude the possibility of some sort of cryptic female choice, since sperm competition and cryptic female choice are not mutually exclusive processes.

#### (c) *Concluding remarks*

Numerous workers have shown a positive correlation between mating success and male body size in water striders and have argued that sexual selection favours large males in this group (e.g. Arnqvist 1992; Sih & Krupa 1992; Fairbairn & Preziosi 1994; Arnqvist *et al.* 1996; Preziosi & Fairbairn 1996). Despite large males having a clear mating advantage, no correlation between mating success and reproductive success was found in this study. This result suggests that the relationship between male body size and reproductive success is more complex than previously thought and also highlights the weakness of measurements of male reproductive success based solely on mating success. Clearly both pre- and post-copulatory processes should be considered when exploring the consequences of sexual selection.

When estimating post-copulatory sexual selection it is also important to create a mating situation in the laboratory as similar as possible to that in nature. Most studies of intraspecific variation in male relative fertilization success were performed with virgins allowed to mate only once (e.g. several studies cited in Simmons & Siva Jothy (1998)). These studies did not consider behavioural differences between males, and the fact that males mate repeatedly in the field. By doing so I show here that post-copulatory sexual selection favours small males, most likely due to a trade-off between mating frequency and ejaculate size. Effects of such trade-offs would pass undetected in traditional double matings and perhaps give the wrong impression of post-copulatory sexual selection favouring large males, especially in species with high mating frequencies.

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