# Why are males bigger than females in pre-copula pairs of *Gammarus pulex*?

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**Summary.** In natural streams, males are bigger than females in precopula pairs of the freshwater amphipod *Gammarus pulex*. A set of experiments is described, the results of which are consistent with the hypothesis that males are larger as a result of a mechanical constraint and not intrasexual competition for mates. Where the male in a pair is relatively larger than the female the swimming performance is superior to those pairs in which the male and female are of similar sizes. This minimises the risk of being washed downstream by the current.

## Introduction

When males are larger than females, in studies of sexually reproducing animals, it is often assumed that the size difference is a result of sexual selection in the form of male-male competition. Larger males, it is argued, have an advantage over smaller males when competing for resources or mates; by extrapolation, males would then evolve to be the larger sex.

Mate guarding is a widespread reproductive tactic in the animal kingdom. In common with some other Crustacea, male *Gammarus pulex* (Linn.) (Malacostraca, Amphipoda) carry the female in pre-copula prior to mating which occurs shortly after the female has moulted. During the pre-copula phase the female is held beneath the male who performs almost all swimming movements. Males and females in pre-copula are matched for size, i.e. there is assortative mating. In pairs collected from streams, males are invariably larger than females (own data) and the mean ratio of male to female length is about 1.3 (Birkhead and Clarkson 1980) despite extensive overlap in size range between the sexes.

Birkhead and Clarkson (1980) suggested that male-male competition has resulted in the evolution of pre-copulatory guarding and that intra-sexual competition might also account for size dimorphism in pre-copula pairs of *G. pulex* since larger males are more likely to breed than smaller ones. However, they could not detect any form of male-male competition which could be implicated in the evolution of larger males. In this note we question the assumption concerning male-male competition and describe an experiment which indicates that the occurrence of relatively larger males could be the product of a mechanical constraint. Specifically, we test the hypothesis that the male is larger in order to swim effectively whilst carrying the female and hence minimise the risks of being washed downstream by the current.

## Materials and methods

Samples of *G. pulex* were collected from the River Pont, Northumberland (grid ref: NZ 166730) and stored in large, aerated laboratory tanks at room temperature. Pre-copula pairs and individual *G. pulex* were removed from the tanks and transferred to individual dishes and, after a 24 h rest period, tested in an experimental stream. The experimental stream is contained in a perspex channel with a square cross-section 20 cm wide; the water depth was kept constant at 10 cm during the experiments. All tests were carried out along a 150 cm straight section of the channel. The stream impeller is linked to a variable speed drive with a large gear ratio. This variable drive allows speeds to be changed smoothly or maintained at known and repeatable values.

Animals were released into the channel at the end of the straight with the stream at its lowest possible speed. In virtually all cases (see below) the animals immediately orientated themselves to swim upstream and began to move against the flow close to the floor of the channel. The speed of the stream was then gradually and regularly increased. While one of us controlled the motor, the other followed the progress of the test animal; observations on actual performance and changes in stream speed were thereby made independently.

Animals were allowed to swim until a stream speed was reached at which they were just starting to move backwards

relative to the channel floor. The speed at this point and the distance travelled were recorded and the animals were transferred to a numbered bowl. The majority of animals were weighed and measured immediately after testing. Some pairs were separated and rested for a further period. The males were then tested again to compare their performance as singles with that in pre-copula.

## Results

Single *G. pulex* perform much better than pairs in pre-copula both for distance travelled up the channel and for maximum stream speed reached during the trial ($N = 67$ singles: mean distance travelled $= 50.7 \pm 5.2$ cm, 95% C.L., mean speed at reversal $= 20.4 \pm 0.5$ cm/s; $N = 53$ pairs: distance $= 28.3 \pm 4.4$ cm, speed $= 14.7 \pm 0.7$ cm/s). No individual *G. pulex* was 'reversed' by a speed less than the modal value at which pairs achieved their maximum. A more direct comparison can be made between single and paired males by examining the performance of those with and without the loading effect of carrying a female in pre-copula, using the data from those males tested in both states. The test group of males is comparable to the total pool of animals. Males perform significantly less well when carrying a female than when swimming alone (paired t-test: $N = 13$, mean speed in pair $= 16.4$ cm/s, mean speed as single $= 20.2$ cm/s; $t = 4.67$, $P < 0.001$).

It was clear from our observations of the performance of pre-copula pairs that the female rarely made any contribution to the swimming effort. While the male could be seen to extend his abdomen into a straight, active posture (not always seen in animals swimming in static bowls) the female usually remained curled up as a dormant load. In the case of pairs where the female was of a similar length to the male, her bulk appeared to actually impair his swimming movements and sometimes prevented normal upstream orientation.

In order to test the effect of relative female size on male swimming performance, we compared the maximum forward speed of pre-copula pairs with the ratio of male and female lengths (Fig. 1). Those pairs in which the male was relatively large compared to the female continued to move up-channel at higher stream speeds than pairs in which the male and female were of a similar size ($N = 53$: $r = 0.43$, $P < 0.002$).

To control for the possibility that this effect is due to the absolute size rather than the relative size of the male (though such a result would contradict data on singles) we compared the maximum speed attained with the difference between the actual male size and that expected from the size of
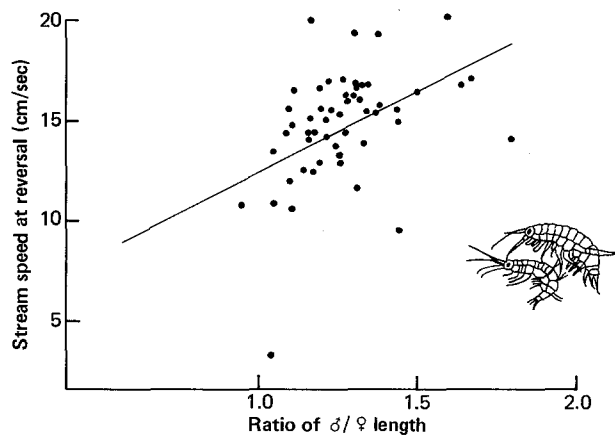


**Fig. 1.** Maximum stream speeds at which pre-copula pairs of *Gammarus pulex* were able to make forward progress. ($N = 53$: $r = 0.43$, $P < 0.002$)

the female; the relationship remains highly significant ($N = 53$: $r = 0.44$, $P < 0.002$). There is, in any case, no overall correlation in these data between the male and female size in pre-copula ($N = 53$; $r = 0.23$, $P > 0.1$). This is in contrast to the natural, assortative pattern and is probably a result of pairs forming in static water in the laboratory tanks.

## Discussion

The results are consistent with the hypothesis that the mechanical constraint of loading on male swimming performance is a satisfactory and adequate explanation for the relatively large size of male *Gammarus* pulex. An alternative explanation, that the dimorphism is due to male-male competition, could not be substantiated by Birkhead and Clarkson (1980).

We have shown that single *G. pulex* can continue to swim upstream against currents that are comparable to those measured at the field site. Their performance is better than that of males in pre-copula and the size of the male in relation to the female is crucial in determining the performance of the pair (Fig. 1). When males and females are closely matched for size, the pairs can withstand and swim successfully only against comparatively gentle currents. This mechanical constraint is probably the product of two factors. Firstly, relative loading; the male may have insufficient power to transport a relatively large mass. Secondly, interference: in closely matched pairs the effective large female size extended close to the male abdomen may restrict his movements during swimming.

The impairment of swimming performance in pre-copula pairs has a number of implications for

the evolution of (i) sexual size dimorphism and (ii) the optimal reproductive sizes of the sexes in relation to assortative mating. It is not surprising that in pairs collected from streams males are invariably larger than females, given the correlation between body size ratio and swimming performance (Fig. 1). It is in the female's interest to pair with a male larger than herself, but while males should always pair with relatively small females, given the constraints on swimming ability, they should also attempt to pair with the largest possible female: larger female *Gammarus* produce more eggs than smaller ones. The pattern of assortative mating found in *G. pulex* may thus be a compromise for the male between minimising the risk of swimming impairment and maximising the numbers of eggs he fertilises.

Recent discussions of sexual size dimorphism have paid little attention to the potential significance of mechanical or loading constraints on relative male and female sizes (but see Wheeler and Greenwood 1983) particularly in species where males are larger and/or in conflict. Males are larger than females in species of Hymenoptera where the male carries the female in a mating flight (Darwin 1874). The ability to fly with the female may, presumably, have involved loading constraints analogous to those experienced by male *Gammarus*. Where load bearing is the responsibility of the female in addition to the burden of eggs, i.e. she carries her mate (a copulatory position widespread in the animal kingdom), we might expect the female to have evolved as the larger sex.

## References

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