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 trans-
ferred 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 trav-
elled = 50.7 ± 5.2 cm, 95% C.L., mean speed at re-
versal = 20.4 ± 0.5 cm/s; *N* = 53 pairs: distance =
28.3 ± 4.4 cm, speed = 14.7 ± 0.7 cm/s). No individ-
ual *G. pulex* was 'reversed' by a speed less than
the modal value at which pairs achieved their maxi-
mum. A more direct comparison can be made be-
tween 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 per-
formance of pre-copula pairs that the female rarely
made any contribution to the swimming effort.
While the male could be seen to extend his abdo-
men 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
prevent 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 con-
tradict data on singles) we compared the maximum
speed attained with the difference between the ac-
tual male size and that expected from the size of
the female; the relationship remains highly signifi-
cant (*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 ade-
quate explanation for the relatively large size of
male *Gammarus pulex*. An alternative explanation,
that the dimorphism is due to male-male competi-
tion, could not be substantiated by Birkhead and
Clarkson (1980).

We have shown that single *G. pulex* can con-
tinue 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 perform-
ance of the pair (Fig. 1). When males and females
are closely matched for size, the pairs can with-
stand and swim successfully only against compar-
tively gentle currents. This mechanical constraint
is probably the product of two factors. Firstly, rel-
ative loading; the male may have insufficient
power to transport a relatively large mass. Second-
ly, interference: in closely matched pairs the effec-
tive large female size extended close to the male
abdomen may restrict his movements during swim-
ning.

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