

SEXUAL SELECTION IN FRESHWATER AMPHIPODS (*GAMMARUS MINUS*)

Brian Dinning, Harry DeButts, Amy Marshall and Amanda Spittel

ABSTRACT

This study attempted to find evidence for sexual selection on body size in the freshwater amphipod *Gammarus minus*. We tested three hypotheses: (1) amplexing males should be larger than single males, (2) amplexing females should not differ in body size from single females, and (3) there should be a positive correlation between male size and female size among amplexing pairs. Populations of amphipods exposed to different levels of fish predation were compared in order to test whether body size is influenced by sexual selection independently of the effect of predation. Four springs were selected - two with fish predators and two without. Statistical analyses showed that males in fish springs are significantly smaller than those in fishless springs. In all four springs, amplexing females were significantly smaller than single females. Also in all four springs, there was a significant positive correlation between amplexing male and female body size.

Keywords: Amphipods, freshwater spring, Gammarus minus, precopula

INTRODUCTION

Amphipods are small crustaceans widely distributed in many freshwater springs throughout central Pennsylvania. They typically occur in high densities in aquatic vegetation (Wellborn 2000). They are on average 5-20 mm in body length. One species in particular, *Gammarus minus*, is usually abundant in cooler, alkaline hardwater springs. Amphipods are not generally found in acidic springs due to lack of calcium for carapace development. The acidic softwater can also cause problems in maintaining energy and ionic balance (Glazier 1999). The abundance and year-round availability of *G. minus* make this species amenable to many kinds of ecological and evolution studies.

Sexual selection, a special form of natural selection, involves competition for mates (Glazier 1999). The better the individual is at obtaining mates, the more offspring it produces and, therefore, the higher its evolutionary fitness. This is because more of the individual's genes will be passed onto their offspring. In male *G. minus* mating success is increased when it has a larger body size and stronger defenses (Glazier 1999). During amplexis (precopulatory guarding) the male carries the female beneath him for several days until she molts. As soon as this occurs, the male fertilizes the female's eggs. The female then carries the eggs in her brood pouch for a few weeks, and after the young leave the pouch, the female is ready to amplex with a male again (Glazier 1999).

In aquatic amphipods and isopods that engage in amplexis, males tend to be larger than females. Therefore, it is believed that sexual dimorphism is the result of sexual selection (Wellborn 2000). The larger males usually out-compete the smaller males for amplexing with females. The larger males are also better at carrying females through fast waters. Because body size is passed on from generation to generation, competition for mates leads to the evolution of larger males. However, predation may affect the body size of *G. minus*, as well (Glazier 1999). The more visual predators (e.g., fish) there are in a stream, the less likely a large male will survive because they are easily observed and eaten. We also considered female body size because recent work suggests that female traits may affect assortative mating and amplexus duration in amphipods, as well (Wellborn 2000).

We examined how predation affects the body size of amphipods during amplexus by studying populations in springs with and without visual predators. We hypothesized that adult males in precopula should be larger, on average, than adult males not in precopula; that there should be no difference in body size between amplexed females vs. non-amplexed females; and that there should be a positive correlation between male and female body size in precopula. We also hypothesized that the males in predatory springs should be smaller than those in non-predatory springs.

FIELD SITE

During March 18-27, 2003, *Gammarus minus* were sampled in two freshwater springs with fish (Blue and Ell) and two without (Emma and Petersburg) in Central Pennsylvania. Blue and Ell springs contained numerous sculpins (*Cottus cognatus*). Fish were absent in Emma and Petersburg springs, though a few predatory salamanders may be present. All of the springs were alkaline ($\text{pH} > 7$) and had water temperatures between 7-12 °C (Table 1).

METHODS AND MATERIALS

We collected 50 amplexing pairs along with 50 single males and 50 single females by dip-netting. The males and females were immediately separated in individual containers. In the lab, they were anesthetized in carbonated water to facilitate body-length measurements (base of the antenna to the tip of the telson; $\pm 1\text{mm}$).

Two-sample t-tests were performed to determine any significant differences in body size between amplexing and non-amplexing amphipods. A correlation analysis was performed to determine whether there were any significant correlations in body size between males and females in amplexed pairs.

RESULTS

In the two springs with fish (Blue and Ell), the mean length of the amplexing males was not significantly different from that of the single males (respectively $t = 1.85$, $P = 0.067$; $t = 1.38$, $P = 0.175$; see Table 1). However, in both of these springs the mean length of the amplexing females was significantly smaller than the mean length of the single females ($t = 3.87$, $P < 0.001$; $t = 2.97$, $P = 0.004$). In the two springs without fish (Emma and Petersburg), the mean length of the amplexing males was significantly larger than that of the single males (respectively $t = 3.04$, $P = 0.003$; $t = 3.12$, $P = 0.002$). But again the mean length of the amplexing females was significantly smaller than the mean length of the single females (respectively $t = 3.64$, $P = 0.000$; $t = 2.24$, $P = 0.028$).

In all of the springs, female-body size covaried positively with male-body size (all $P < 0.05$; Figs. 1-4). The slopes of these linear relationships were higher in the fishless springs (Figs. 3 and 4) than in the fish springs (Figs. 1 and 2).

Table 1. Water temperature and pH, mean body lengths of amplexing and single male and female amphipods (*Gammarus minus*) in two springs with fish and two without. P-values for comparisons of amplexing and single amphipods and for correlations between male and female body length in amplexing pairs are also indicated.

Spring	Temp (°C)	pH	N	Mean (mm)	SD (mm)	p-value (2-sample t-test)	p-value (correlation test *)
Blue (with fish)	9.7	7.08					
Single Male			50	8.20	1.18	0.067	coeff = 0.343 p = 0.015
Paired Male			50	8.62	1.09		
Single Female			50	5.70	0.79	0.000	
Paired Female			50	5.10	0.76		

EII (with fish)	9.8	7.51					
Single Male			50	7.84	1.35	0.175	coeff = 0.632 p = 0.003
Paired Male			20	7.40	1.14		
Single Female			50	5.00	1.12	0.004	
Paired Female			20	4.35	0.67		
Emma (without fish)	7.5	7.50					
Single Male			50	9.92	1.55	0.003	coeff = 0.637 p = 0.000
Paired Male			50	10.82	1.41		
Single Female			50	7.68	1.39	0.000	
Paired Female			50	6.66	1.41		
Petersburg (without fish)	11.8	7.82					
Single Male			50	8.42	1.43	0.002	coeff = 0.530 p = 0.000
Paired Male			50	9.14	1.18		
Single Female			50	5.86	0.88	0.028	
Paired Female			50	5.46	0.91		

Bold signifies a significant difference.

* Correlation between male and female body size in amplexing pairs.

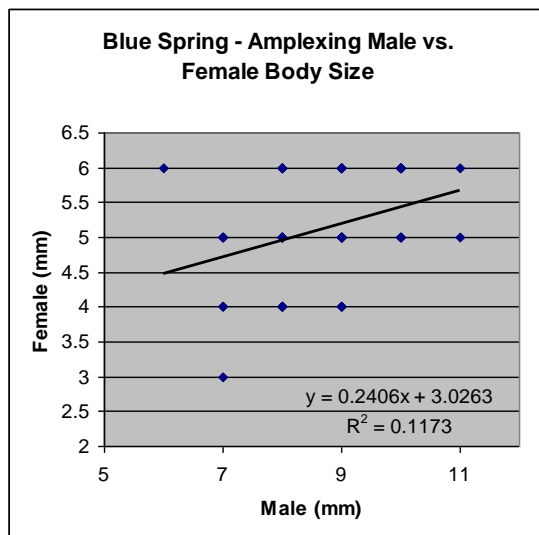


Figure 1. Female body length in relation to male body length of amplexing pairs of *Gammarus minus* in Blue Spring (March 18, 2003).

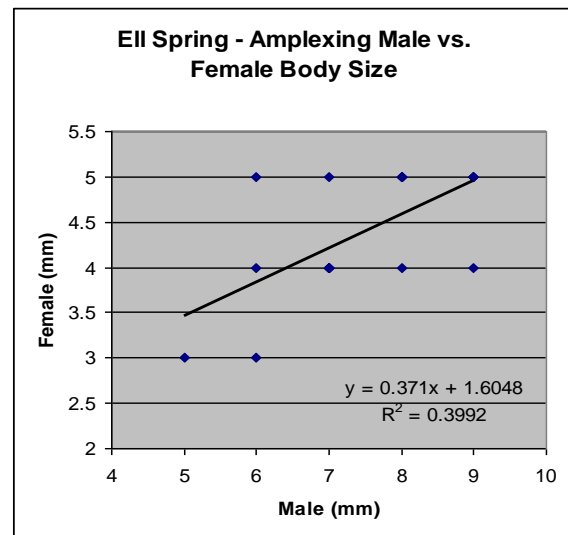


Figure 2. Female body length in relation to male body length of amplexing pairs of *Gammarus minus* in EII Spring (March 27, 2003).

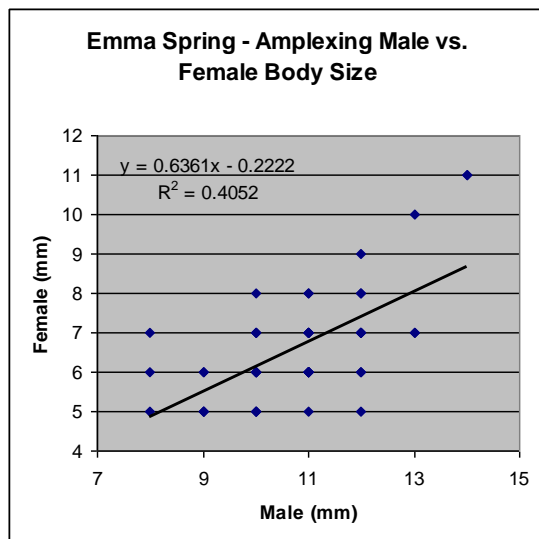


Figure 1. Female body length in relation to male body length of amplexing pairs of *Gammarus minus* in Emma Spring (March 25, 2003).

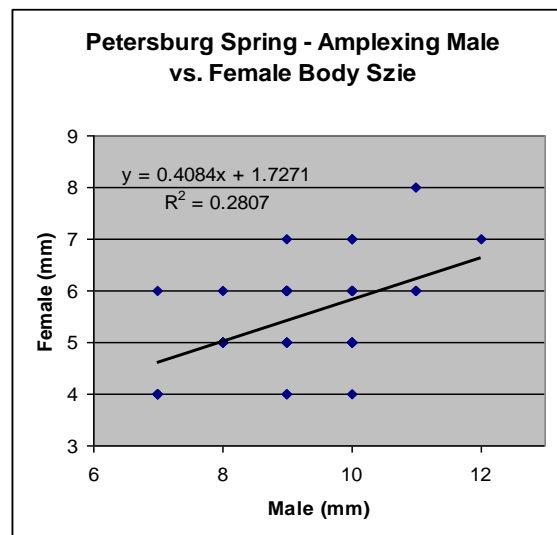


Figure 2. Female body length in relation to male body length of amplexing pairs of *Gammarus minus* in Petersburg Spring (March 25, 2003).

DISCUSSION

The first hypothesis, that the amplexing males should be larger than single males, was not supported in either of the springs with fish, as there was no significant difference in body length between amplexing and single males in Blue and Ell springs. However, amplexing males were significantly larger than single males in the springs without fish (Emma and Petersburg), thereby supporting the hypothesis. The second hypothesis, that there should be no significant difference in body length between amplexing and non-amplexing female amphipods, was falsified because the amplexing females were significantly smaller than the single females in all four springs. However, the third hypothesis that there should be a positive correlation between body size of male and female amphipods in precopula was shown to be true in all springs.

Fish predation may be responsible for why significant body-size differences between amplexing and single males were found in the fishless springs, but not in the fish springs. The fish may have selectively preyed on the larger males, thus counteracting sexual selection for larger size in the males living in fish springs. This explanation is consistent with the observation that males were significantly smaller in the springs with fish than without fish.

In contrast, amplexing females were smaller than single females in all four springs with or without fish. Perhaps their smaller size made them less vulnerable to fish predation, but this hypothesis is contradicted by the observation that females were smaller in the fish springs than in the fishless springs, as were the males.

Lastly, in all four springs larger males tended to be paired with larger females perhaps because they had to be bigger in order to carry females during amplexus.

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LITERATURE CITED

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