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Advantages and a disadvantage of large size for male *Gammarus pulex* (Crustacea: Amphipoda)

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Summary. The breeding system of the freshwater amphipod *Gammarus pulex* includes a precopulatory guarding phase by a male. The length of this guarding phase is investigated with respect to a male's size and the number and size of his competitors. As the absolute number of competitors increases, so does the guarding time but as the absolute number of available females increases, the guarding time decreases. Takeovers of the females by unpaired males are more frequent in longer precopulas (Table 2). In contests for females, larger males have two advantages over smaller males; they are better able to make a takeover (Table 2) and better able to resist takeover attempts while paired (Table 3). Males increase the length of the guarding phase as the mean size of their competitors increases (Table 4). When not paired males are usually searching for available females, perhaps in the stream current. Females are unaffected by current speed but increasing current causes decreased male survivorship (Table 5) and increased precopula duration (Table 5). Searching in currents is more dangerous for larger males than smaller ones. It is proposed that the male size distribution observed is the result of selection pressure to increase size from male-male competition balanced by selection against large size while searching for females in the current.

Introduction

In recent years the interest of evolutionary biologists has been drawn to differences in behaviour between individuals. This has been due in large part to the development of the theory of Evolutionarily Stable Strategies (see Maynard Smith 1982), which has shown that different behavioural strategies can coexist within a single population. In the competition for scarce resources, as between males for females, all individuals are not equally successful and theory has suggested that an individual's behaviour should vary with its phenotype. Thus, instead of all animals showing the same behaviour and achieving differing degrees of success, individuals of different phenotypes may be selected to show different behaviours, with each phenotype attempting to maximise its own success (Parker 1982).

Animal size can vary considerably within populations and has been shown to be important in reproductive success in a variety of species (e.g., Davies and Halliday 1977) for *Bufo bufo*, Partridge and Farquhar (in press) for *Drosophila melanogaster*, Ridley and Thompson (1979) for *Asellus aquaticus*). However few studies have considered how behaviour varies with size. One aim of this paper is to describe how a male's size and the number and size of his competitors and potential mates influence mating decisions in the freshwater amphipod crustacean *Gammarus pulex*. In the majority of species, larger males are more successful than are smaller males in aggressive interactions. However, if a species is at some equilibrium for size, then there must also be counter-balancing selection against large size. The second aim of this paper is to describe such a selection pressure in *G. pulex*.

The mating system of *G. pulex* includes a precopulatory guarding phase by a male during which he grasps the female and carries her around for some days until she moults (see Birkhead and Clarkson 1980; Hynes 1955). During this phase, unpaired males may attempt to take over a female by displacing the paired male. When the female has moulted, the pair copulates and separates. The

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female then lays her eggs into a brood pouch where they are fertilised by the male's sperm. The eggs are carried in the pouch as they develop and active young are released. When in breeding condition a female will normally produce a brood at each moult. It is the length of the guarding phase which is investigated here. Hughes (1979) states that sex ratio influences precopula duration but his methods confound sex ratio and density. There are 5 experimental sections; the 1st deals with the effects of altering the number of competitors and potential mates present for a male, the 2nd, in two parts, how male size influences the probability of a takeover occuring and the 3rd the effects of varying the mean size of the competitors present.

G. pulex are normally found under stones in the beds of streams and it is here that the majority of the competitive interactions between males will take place. There is very little current beneath the stones (Hynes 1970). However, both sexes must sometimes move between stones in search of food or mates and this will expose them to the current flow. Artificial streams were used to investigate whether the sex or size of an animal influence how well it can move in the current. The 4th experimental section deals with a situation containing both males and females and the 5th one where only males were present.

Materials and methods

Gammarus pulex were collected from a stream near Hawarden, North Wales (National Grid Reference SJ 649312) on a single occasion for each experiment by kick sampling (Hynes 1955). In the laboratory the animals were kept in holding tanks at 10 °C and at a photoperiod of 12 h light:12 h dark with constant aeration until required, which was always within a few days.

Pairs already in precopula were removed from a sample and the remaining animals anaesthetised with 2-phenoxyethanol to be sexed and measured. Sexing is by the presence of penal papillae for males and eggs in the brood pouch for females; this ensures all animals used were mature and the females in breeding condition. Length was measured from the base of the first antennae to the base of the telson to the nearest mm below, with the animal straightened over graph paper. Only animals of the sizes found in precopula when the sample was taken were used; males were from 9 to 16 mm and females from 7 to 11 mm. The animals were then left overnight to recover fully from the anaesthetic. For the 1st experiment, they were then anaesthetised again and marked with a small spot of matt paint on the dorsal side of the thorax, for the 2nd, liquid paper was used for marking. In either case, each animal in a dish was individually recognisable. Marking does not appear to harm or hinder the animals in any way. If necessary, animals were remarked 3 days after a moult once the cuticle was sufficiently hard to permit handling without damage.

The first 3 experimental sections were conducted in dishes or cups containing small pieces of gravel, stream water and food to excess. The food used was shredded leaves, elm, plane and sycamore, and the water was changed every 10 to 14 days. The containers were examined daily and it was recorded if any animals were in precopula, if a takeover had occurred and if any animals had died or moulted. If an animal died, it was replaced with another of the same sex and as close as possible to the same size. This was also done for animals which moulted in the 1st section; in the 2nd the animals were remarked. The duration of a precopula was taken as the time from the pair being formed until the female moulted and the pair separated.

For the 4th and 5th sections, three artificial streams were set up. Each was a fibre glass trough (162.5 × 23 × 21.5 cm) placed at an angle on scaffolding). One of the streams was maintained without a water current but with a similar depth of water to the other two streams. In the others, water was supplied from a plastic header tank (180 l). Water from a larger reservoir tank (320 l) was delievered to the header tank via 3 cm internal diameter PVC tubing by a plastic and stainless steel submersible pump. The pumps used delivered different amounts of water to the header tanks and as no water built up in these this resulted in a different current speed in each trought. The current speeds were measured with a Novonic Stream Flo probe and were 6 cms^{-1} at the surface of the centre of stream 1 and 4 cms^{-1} in a similar position in stream 2. The still trough was stream 3. At the lower end of each trough a plastic screen, mesh size approximately 1 mm, stopped movement of animals down into the reservoir tank. The outflow of stream 3 was blocked. The streams were housed in a cool, well-ventilated basement room. The water was taken from the same stream as the *Gammarus*. The temperature of the water was measured repeatedly during the experiments and varied from 16 to 19 °C with the streams never differing by more than 1.5 °C. The photoperiod was controlled at 16 h light: 8 h dark. Each stream had approximately 2 cm of standard aquarium gravel spread evenly on the trough bottom and three large stones from the stream evenly spaced down the length. The streams were allowed to equilibrate for 3 days before each experiment.

For the 4th experimental section, 100 unpaired males were released at the centre of each stream. Also released were 60 females. The streams were then run for 15 days with the only interference being that of checking the water temperature and current speed and topping up the reservoir to balance evaporation losses. At the end of this time, the pumps were turned off and the streams completely cleared and the animals all removed. Unpaired animals were killed in alcohol and their size measured. Each pair was placed in a plastic cup with 75 ml stream water and a piece of gravel and observed daily until the female moulted and the pair separated. The animals were then killed and their size measured.

For the 5th experimental section the large stones were removed from the streams. This was done to minimise the shelter available to the animals and so maximise their exposure to the current. Ninety five males were released into each stream as before and each stream received an identical size distribution of animals; the mean size was 10.3 ± 1.0 mm. The streams were again run for 15 days and the surviving animals removed, killed and measured.

All statistics are presented as mean ± SD.

Results

The effects of the number of competitors and females

Ten replicates of each of four densities of animals were set up in dishes 14 by 8 cm with approximately 150 ml of water, a few pieces of gravel and food. The four densities used were two, four, eight and twelve animals per dish and in all cases there were equal numbers of males and females. The dishes were placed in a randomised block pattern in the coldroom.

During this experiment two females were observed to moult without having been taken into precopula. Two females were abandoned before moulting by the males which had been carrying them, approximately 2% of precopulas initiated. Two females died while in precopula and were not released immediately by the males, who continued to carry them for 1 and 5 days. These numbers are too small to reach any definite conclusions on.

Fighting for females was frequently observed during the daily inspections. Most of these fights are very brief but occasionally they are prolonged and vigorous. The paired male kicks at the attacker while attempting to hold the female away from him. Occasionally the attacker will succeed and take over the female. The significance of these fights is considered in the later series of experiments.

Some of the precopula durations must be excluded from the analysis as the animals were in precopula the day after that on which they had been placed together and so the precopula may have begun earlier had this been possible. This happened on 23 occasions. A further 11 precopulas must also be rejected because the male was paired with the female on the day immediately after having been paired with a different female, which had just moulted, and so this may not have been the first day on which that female would have been acceptable to that male.

Seventy precopula durations remain to be analysed. The duration was taken as the total duration even if a takeover occurred as it is the decisions of the original male which will have determined the total duration. The factors influencing precopula duration were analysed by multiple regression using the regression subprogram of the Statistical Package for the Social Sciences Version 8 (Kim and Kohout 1975). The precopula duration was used as the dependent variable throughout. The sizes of the original male and of the female were used as two of the independent variables. The others were possible parameters that males could use to make their mating decisions and were used in various combinations to find the best fit to the data: the number of unpaired males and females, the total numbers of males and females and the number of males smaller than, the same size as and larger than the male which went into precopula. Various transformations (e.g. log) and composite variables (e.g. sex ratio) were also assessed for the day on which the first male took a female into precopula.

Table 1. Summary table of variables used in regression analysis in section 1. $n = 70$ in all cases

Variable	Mean	SD
Precopula duration (days)	7.3	4.1
Male size (mm)	12.9	0.9
Female size (mm)	9.1	0.7
Number of unpaired males	3.8	1.5
Total number of females	4.6	1.7

The best fit to the variation in precopula duration was given by using male size, female size, the number of unpaired males and the total number of females. A summary of these variables is presented in Table 1. In fact, no combination which did not include these last two yielded a regression which was significantly different from the null hypothesis. The individual coefficients of the animals' sizes were not significantly different from zero and so these are not included in the regression equation below. The regression equation was $y = -1.3$ (total number of females) $+ 1.7$ (number of unpaired males) $+ 6.8$. This equation departs significantly from the null hypothesis ($F_{2.67} = 3.3$, $P < 0.05$) and the individual coefficients were also significantly different from zero ($F_{2.67} = 5.1$, $F_{2.67} = 6.7$ respectively, both $P < 0.01$).

Two further points must be made about the regression equation above. The two factors were found to strongly interact in that the first into the regression model was not significant on its own but only became so when the other was added. Thus both factors must be assessed to make an accurate prediction of the animals' behaviour. Secondly, no composite of the variables yielded a significant result in any combination used. This is particularly important when considering a factor such as sex ratio. It may be that this is not a useful single measure due to the strong interaction of its component variables, the numbers of males and females present.

Seventeen takeovers were observed, only 16 of which are eligible for analysis as one was in a 'first day' precopula. These 16 involved 14 females, two were subject to two takeovers, out of 70 precopulas observed and this gives a probability of 22% that a male will lose a female before her moult. This seems very high and must be a significant influence on precopula duration. In fact, those precopulas in which there were takeovers were significantly longer than those in which there were no takeovers

Table 2. Sizes of animals and precopula durations in 1st takeover experiment. $n=166$ for animals not involved in takeovers and $n=16$ for takeovers. Significance levels derived from t-tests

	Precopula duration (days)		Size of male in precopula (mm)		Size of other male (mm)		Size of female (mm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Takeovers	10.1	6.5	12.1	1.0	11.9	1.0	8.3	1.0
No takeovers	6.8	4.2	11.6	1.0	11.3	1.0	8.8	0.8
Significance level	$P<0.001$		n.s.		$P<0.01$		$P<0.02$	

(9.1 ± 4.0 days and 6.7 ± 4.1 days respectively, $t=2.0$, $P<0.05$). It is possible that takeovers somehow interfere with the female and so delay her moult. However, the two females subject to two takeovers did not moult significantly later than those subject to one (8.0 ± 5.7 days and 9.3 ± 3.9 days respectively, $t=0.4$, $P>0.05$). Therefore it would seem that the longer a precopula lasts the more likely there is to be a takeover during it. The simplest explanation of this is that there is a constant probability of the male losing the female per unit time. However, there was no evidence here to suggest that the male's size influences the probability of a takeover occurring. The sizes of males making takeovers (12.6 ± 0.8 mm, $n=16$) was not significantly different from the sizes of males losing females (12.9 ± 0.9 mm, $n=16$) ($t=1.1$, $P>0.05$) nor was the size of males losing females significantly different from the size of those entering precopula (12.9 ± 0.9 mm, $n=70$) ($t=0.0$, $P>0.05$). The size of the male in a pair does not influence the length of a female's moult cycle (Ward, in preparation).

Male size and the probability of takeover

It is possible that the absence of any relationship between male size and the probability of a takeover occurring was due to the rather small of takeovers observed. Ridley and Thompson (1979) report that for *Asellus aquaticus*, an isopod with a similar precopulatory guarding phase, the larger the ratio between the attacking and the defending males' sizes, the more likely a takeover was to occur. This could be due either to larger males being better able to make a takeover or being better able to resist takeover attempts while paired than are smaller males. Two experiments were conducted to investigate these possibilities in *G. pulex*.

Male size and the ability to make takeovers

Two males and one female were placed in a plastic cup with a piece of gravel, excess food and approximately 75 ml of stream water. If both males had moulted and were unmarked than the cup was discarded.

No females were abandoned before they moulted or moulted without having been taken into precopula in this experiment. One hundred and eighty two precopulas were observed and takeovers occurred in 16 (9%). This is a smaller proportion than in the previous experiment probably because there were fewer unpaired males per cup to make takeover attempts. The sizes of the animals involved and the precopula durations are presented in Table 2. As expected from previous work where larger males were found to guard females for longer than smaller males before the female's moult (Ward, in press), the males which went into precopula initially were significantly larger than the other males ($d=2.8$, $P<0.01$). Also, as in the previous experiment, takeovers occurred in the longer precopulas. The sizes of males which did or did not lose their females were not significantly different. However, the males making takeovers were significantly larger than those failing to do so.

The females which were taken over were significantly smaller than those which were not. This may mean that males are more likely to give up a smaller female than a larger one as the attacking male presumably has very little information as to the size of the female as the normal initial assessment is impossible and the defending male attempts to prevent him even contacting her.

Male size and the ability to resist takeovers

A deficiency in the previous experiment in detecting differences between males of different sizes in the ability to resist takeovers was that the smaller males were less likely to become paired in the first place. A 2nd experiment was therefore conducted.

A pair which had previously formed was placed in a cup with an unpaired male which was larger than the paired male. The screening of a large

Table 3. Sizes of animals and precopula durations in 2nd takeover experiment. $n=235$ for animals not involved in takeovers, but 44 females were eaten before they could be measured, and $n=24$ for takeovers, 6 females were eaten. This experiment was conducted in two series and so the significance levels are derived from F-tests. There were significant differences in all measures between the series

	Precopula duration (days)		Size of male in precopula (mm)		Size of other male (mm)		Size of female (mm)	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Takeovers	4.9	2.7	10.7	1.0	11.9	1.0	8.1	0.9
No takeovers	4.1	2.6	11.1	0.9	11.7	1.0	7.9	0.7
Significance level	n.s.		$P<0.05$		n.s.		n.s.	

number of animals allowed a wide range of paired male sizes to be used but a much smaller size range of unpaired males. The unpaired males were marked. Paired males only extremely rarely moult before the female and this was not observed here. When the female moulted, all three animals in a cup were killed and measured. This experiment was conducted in two series.

Two hundred and fifty nine precopulas were observed and takeovers occurred in 24 (9%), the same proportion as in the previous experiment. The sizes of the animals involved and the durations of the precopulas are presented in Table 3. There was no significant difference in the durations of the precopulas in which there was or was not a takeover. This was probably due to the much shorter durations involved, on avergae half of the total precopula duration and the variation between the series. Males which lost their females were significantly smaller than those which did not. There was no significant difference in size between those males which did and did not make a takeover. Against attackers of equal size, smaller males are more likely than larger males to lose their females.

Unfortunately, in this experiment the females could not be measured before being placed in the cups and some were eaten by the males soon after their moult. This has resulted in the reduced numbers in Table 3. There was no significant difference in size between those females involved in takeovers and those not. The significant differences in the measurements between the series reflect the differences in the sizes of paired and unpaired animals at the different collection dates and seasonal variation in guarding time found in the field.

The effects of varying the sizes of competitors

As the previous experiments show that males of different sizes have different probabilities of holding a female until her moult and previous work that larger males guard females for longer than do smaller males (Ward, in press), the question arises whether males can alter their guarding behaviour with respect to the mean size of their competitors. The following experiment was conducted to test this possibility.

Three large tanks were set up with a gravel bottom, an abundance of food, approximately 4 l of water and constant aeration. Into each of these were placed 90 males with the following size distributions; tank 1: 30 10mm, 30 11mm, 30 12mm; tank 2: 30 11mm, 30 12mm, 30 13mm; tank 3: 30 12mm, 30 13mm, 14mm. Also into each tank were placed 30 females of random sizes which had been unpaired. The tanks were then left for 20 days. At the end of this time, they were cleared and all the animals removed. Unpaired animals were killed and their size measured. Pairs were placed individually in cups until separation, when the animals were killed and measured. The sizes of paired and unpaired males and females recovered and the precopula durations are presented in Table 4. There was some mortality in the tanks. However, the numbers of males alive and dead did not differ significantly among the tanks ($\chi_2^2=3.9$, $P>0.05$), nor did those of females ($\chi_2^2=3.0$, $P>0.05$). Again, some of the paired females were eaten before they could be measured. There were no significant differences among the tanks in the sizes of the remaining females ($F_{2.76}=3.0$, $P>0.05$). All the unpaired females were carrying eggs or young in their brood pouches. As expected, there was a significant difference among the tanks in male size ($F_{2.217}=66.7$, $P<0.001$).

A 13 mm size class male was found paired in tank 1. Either this animal had moulted and grown during the experiment or an error had been made in the initial measurement. This animal was nevertheless used in the following analysis; indeed, its presence made the analysis broader than the experiment had been designed for. Only those pairs which remained together until the females moulted

Table 4. Sizes of paired and unpaired males and females recovered and precopula durations from each tank in section 3 after 20 days. The guarding times are for males of size classes 12 and 13 mm *only*

Tank	Male size (mm)						Female size (mm)			Precopula duration (days)		
	Paired			Unpaired								
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1	11.5	0.8	8	10.8	0.8	71	8.6	0.7	27	5.0	0.0	3
2	12.1	0.6	14	11.6	0.8	58	8.2	0.7	30	8.5	4.8	11
3	12.7	0.7	19	12.4	1.0	50	8.3	0.8	22	13.2	6.1	12

Table 5. The sizes of animals recovered and precopula durations from each stream in section 4

Stream	Paired						Unpaired						Precopula duration (days)		
	Male size (mm)			Female size (mm)			Male size (mm)			Female size (mm)					
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1	11.1	1.1	7	8.6	0.5	7	10.8	1.1	49	8.1	0.8	48	4.3	2.7	7
2	11.3	1.0	13	8.4	1.0	13	10.7	2.0	55	8.0	0.8	42	2.4	1.3	13
3	11.6	1.0	16	7.9	0.7	15	10.9	0.9	69	7.8	0.7	34	7.4	4.7	16

have been included. Three females were abandoned before their moults and these were all from tank 3, where male-male competition may be expected to be greatest. This may mean that males are more likely to make errors in judging the time to a female's moult when subject to greatest competition for mates; though the rather small number involved rules out a firm conclusion. Also, two females died in precopula, one from tank 1 and one from tank 3, and again these were carried by the males for 1 and 2 days respectively. The differences between the tanks in the guarding times of males of the size classes 12 and 13 mm *only* are significant ($F_{2.22}=3.6$, $P<0.05$). The mean guarding times for the males of size class were 12 mm 8.5±5.5 days and 13 mm 11.6±6.1 days. These are not significantly different ($F_{1.22}=1.6$, $P>0.05$) but are in the expected direction. Thus, males of a given size class guard females longer as the mean size of their competitors increases.

The behaviour of males when females are present in the streams

The numbers and sizes of paired and unpaired animals recovered and mean precopula durations from each stream at the end of this experiment are presented in Table 5. One of the paired females was eaten soon after her moult. Considerable mortality occurred in the streams. The total number of males alive and dead differs significantly among the streams ($\chi^2_2=20.1$, $P<0.001$) with fewest surviving from the fastest stream, stream 1. This is not the case for females, where there was no significant difference among the streams in the numbers surviving ($\chi^2_2=2.8$, $P>0.05$).

There is a trend towards larger mean male size with decreasing current speed, though this in not significant ($F_{2.205}=0.8$, $P>0.05$) but the paired males are significantly larger than the unpaired males ($F_{1.205}=7.9$, $P<0.01$), as expected. There was no significant difference among the streams in female size recovered ($F_{2.155}=2.0$, $P>0.05$) or between paired and unpaired females ($F_{1.155}=2.6$, $P>0.05$). This latter result is not as expected as larger females are guarded for longer than are smaller females (Ward, in press) and so are more likely to be paired at any particular time. This anomaly is probably due to the rather small number of pairs used here. There was also no significant difference among the streams in the ratio of male to female size in pairs ($F_{2.33}=2.3$, $P>0.05$) suggesting that any ability of males to carry females of different sizes in not important to their survival.

From the results in the first section, we would have expected an increase in mean precopula duration from stream 1 to stream 3 as the number of competing males increased. However, the mean precopula duration is significantly shorter in stream 2 than in stream 1 ($t_{18}=2.2$, $P<0.05$). Thus the faster current in stream 1 has resulted in a longer precopula duration than would be expected in the absence of current. The difference between paired and unpaired males in size also increases with decreasing current speed.

The behaviour of males when females are not present in the streams

The previous experiment showed that current speed influences male survivorship and mating decisions; the faster the current the longer a male is prepared to guard a female. This experiment was conducted to investigate if male size influences survivorship in currents. As there was very little shelter and no females present, the males would have been constantly searching in the current.

The mean sizes of the animals recovered from each stream were: stream 1: 9.5±0.5 mm, $n=8$; stream 2: 9.8±0.6 mm, $n=17$; stream 3: 10.3±0.9 mm, $n=80$. Again, there was considerable mortality during the experiment, particularly in the streams with current. The numbers recovered alive and dead differ significantly among the streams ($\chi^2_2=139.2$, $P<0.001$) as do the sizes of these animals ($F_{2.102}=4.5$, $P<0.05$) with the smallest number and the smallest mean size being recovered from stream 1, where the current was fastest.

Discussion

It is clear that male-male competition is of crucial importance in shaping the reproductive decisions of male *Gammarus pulex.* Males are able to assess the number of competitors and the number of potential mates in their environment. When there are more competitors, males guard for longer both because they are more likely to lose a female per unit time and a female becoming available is more likely to be taken into precopula by another male. When there are more females cycling in the population, a male will be more likely to find one within any given fraction of the moult cycle, if the females remain unpaired, as the females do not appear to be synchronised in their breeding, and so the mean guarding time decreases. Both these changes may give males a constant probability of guarding a female till her next moult. Males regard all females present as potential mates presumably as a takeover may be possible or the male may even abandon the female but regard only unpaired males as direct competitors as these cannot interact with other females while paired. The likelihood of a takeover occurring during a long precopula may set an upper limit to precopula duration and so prevent males simply guarding any unpaired female encountered until her next moult (cf. Grafen and Ridley 1983).

Although some of the changes of ownership of a female observed in the takeover experiments may be due to the original males abandoning the females, the frequency of the changes and the fact that the females were never seen unpaired once a precopula was initiated make it extremely unlikely that the changes were not the results of fights. Larger males have two advantages over smaller males with respect to takeovers; when unpaired they are better able to make a takeover and while paired are better able to resist takeover attempts by unpaired males. It is probably the combination of these advantages which allows larger males to guard females for longer than can smaller males (Ward, in press). Birkhead and Clarkson (1980) concluded that size was not important in takeovers but their conclusion was based on rather small numbers of animals as they only observed animals in this context for 1 day, detecting eight takeovers.

A variety of studies on other species (e.g., *Centris pallida,* Alcock et al. 1977; *Scatophaga stercoraria,* Borgia 1981: *Asellus aquaticus,* Ridley and Thompson 1979) have shown that animals of different sizes may behave differently. However, fewer studies have shown that animals can vary their behaviour when their competitors are of different sizes. The results here show that males of *G. pulex* of a given size guard females for longer when their competitors are larger and so a greater threat to their mating attempts; though how the animals obtain this information is unknown. It may seem surprising that animals can monitor the mean size in the population but as the results of fights depend to some extent on the opponents sizes, it may be that males estimate not their own absolute size but rather their size relative to that of their competitors. This ability will be advantageous for two reasons. Firstly, the sizes of the animals in the population varies over the season (Birkhead and Clarkson 1980) and secondly, *G. pulex* grow throughout life, if slowly as adults (Sutcliffe et al. 1981). The appropriate guarding time for a male to attempt will therefore vary with time and to maximise his success he will have to match his actual guarding time to that required.

In addition, searching costs influence mating decisions. A difference between males and females in survivorship in currents has been found. Females are unaffected by current speed whereas male survivorship decreases with increasing current speed. This must reflect a difference in behaviour between the sexes. Females are selected to convert food into eggs and so only need expose themselves to the current to search for food. As the animals' food tends to accumulate in particular places (Gee 1982) this will not be very often. However, males achieve highest reproductive success by mating with many females and so will have to move between stones more often in search of suitable mates. This will constantly expose them to the rigours of the current as they attempt to prevent themselves being swept away and so suffer a decrease in their survivorship.

As the current speed increases, males guard females for longer. As there is no reason to believe the length of the female moult cycle is affected by current speed, this probably means males are taking the females earlier in their moult cycles. This is another reflection of the dangers to males while searching. Once a male has become paired with a female he can become more or less quiescent until the female moults, as the males perform almost all the movement for a pair. By guarding a female for longer, a male avoids the even more costly behaviour of searching in the current.

Searching in currents is more dangerous for larger males than for smaller ones, though why this should be so is unknown. However, the result is that the difference is size between paired and unpaired males decreases as the current speed increases. Thus as the larger males are increasingly disadvantaged in searching and guard females for longer to secure each mating, smaller males are more likely to obtain a female and so increase their reproductive success.

The male size distribution observed in the population will therefore reflect selection pressures on size from both directions. The success of larger males in male-male competition will tend to increase mean male size but this will be balanced to some extent by the decreased survivorship of large males when searching in the current for food and females.

Two types of error have been detected here which males make when choosing to guard females. Firstly, females are sometimes taken into precopula but later released before their moult. Similar behaviour in *A. aquaticus* has been termed 'intermittent pairing' (Manning 1975). This behaviour may be more frequent when competition is greater. Secondly, when a female dies during precopula the male appears unable to detect this immediately and may carry the body for some time. Presumably the frequency of this is so low that the cost of constantly monitoring the female outweighs the benefit which may be gained. Dennert (1974) reports another type of error made by *Gammarus* males. Males may take females of other species into precopula until the female moults although these pairs are always infertile.

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