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Mate choice for male and female size in aquatic isopod *Idotea balthica*

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In laboratory tests the pair formation of the sexually size dimorphic and colour polymorphic isopod *Idotea balthica* was non-random with respect to size, whereas colouration had hardly any effect on mate choice. When given a choice of two females, 70% of the males selected the larger female for precopula. In experimental populations, however, female size had no evident effect on mate choice, so that further confounding effects may complicate the pair formation in natural heterogenous habitats. Precopulatory males were larger than solitary males in the experimental populations, both in female- and male-biased populations. The larger size of precopulatory males may at least partly result from male-male competition, but the females may also affect the precopulatory success of the males in a size-dependent manner. Consequently, presumably both intrasexual and intersexual interactions favour larger males in I. *balthica*. Female size, on the other hand, may be only a second choice after female maturity. The male-biased sex ratio in early summer may in particular discourage males from being too size selective.

1. Introduction

The mating behaviour of aquatic crustaceans with a prolonged precopulatory phase (Parker 1974), when usually the male carries the female for some time before insemination, offers an excellent opportunity to study the effects of sexual selection on both male and female traits. The significance of the guarding behaviour on size and size differences between sexes has been studied most thoroughly in amphipod gammarids (e.g. Ward 1984, Dunham et al. 1986, Elwood et al. 1987, Greenwood & Adams 1987) and in some isopod species (e.g. Manning 1975, Adams et al. 1985, Veuille 1980, 1986).

The non-random pairing with respect to size often observed in precopulatory pairs may result from different processes which may or may not include sexual selection. At least six hypotheses have been put forward to explain the non-random size distribution of precopulatory males and females:

1) In species where the potential reproductive rate of males exceeds that of females, as in most crustaceans with a long incubation period, the operational sex ratio is male-biased and males compete intensely for mates (Clutton-Brock & Vincent 1991). Male-male competition for access to females may favour large male size (Ward 1984, Elwood et al. 1987). Large males may pair more readily than the smaller ones, and they may also kidnap females from the smaller males (Ridley and Thompson 1985, Dick & Elwood 1990).
2) When males are investing time and energy in precopulatory guarding they can benefit from being choosy (male choice). When the reproductive output increases with female size and the number of mates is limited by guarding time, a male can gain in offspring number by selecting large females (Manning 1975, Ward 1984) and in the number of mates by selecting females near their preparturial moult (Elwood et al. 1987).
3) Female choice for certain male traits is a widely documented phenomenon, for example among birds and fishes (e.g. Kodric-Brown 1990) and is possible also among crustaceans. Females may exercise choices e.g. on male size by resisting precopulatory attempts by males (Ward 1984).
4) Habitat selection may lead to assortative pairing if the different sized animals select different microhabitats and pair mainly within those microhabitats (Birkhead & Clarkson 1980, but see Thompson & Moule 1983).

Hypotheses presupposing

5) male choice and natural selection on swimming performance of the male in the precopulatory pair (Adams & Greenwood 1983, Adams et al. 1985, Greenwood & Adams 1987), or
6) male choice and different duration of the precopula of different sized males due to different guarding costs (Elwood & Dick 1990)

has also been put forward.

We studied the effects of both female and male size on the mate choice of the size dimorphic and colour polymorphic isopod *Idotea balthica* (Pallas). In the present study, we concentrated on male choice in a situation where a male could choose between two different sized females, in addition to pair formation in experimental populations where both the male and the female size of paired and solitary animals were examined. The possible effects of the colour morph on mating decisions were also considered.

2. Materials and methods

2.1. *Idotea balthica*

In the northern Baltic the pairing period of *I. balthica* starts with precopula in early June. Males are the larger sex and guard the females for some days during the period of two to three weeks when the females are in the preparturial moulting stage. The breeding development is well synchronized, with almost all females becoming perceptive to precopula within two to three weeks. In the southern Baltic the synchronicity breaks down and the population consists of individuals in various moulting stages simultaneously.

The copulation takes place during the parturial moult, after which the eggs are laid in the ventral marsupium. After a hatching period of about three weeks the juveniles are released and the next brood is laid in the marsupium. In the northern Baltic the juveniles mature the following June at the age of 10 to 12 months, but in the southern Baltic the juveniles born in early spring may mature during the same season (Kroer 1989). It is not known whether the fertilization of the broods following the first one requires further copulation or whether the females are able to store sperm from the first copulation. The only evidence that we have from the southern Baltic supports the first possibility (unpubl.). When the broods of gravid females were removed, new broods were observed among the previously aborted females reared with males, but not among those reared without males.

2.2. Male choice experiment

The behavioural experiments for selection of female characteristics were carried out at the Kämpinge Marine Biological Research Station in S. Sweden (55°25'N, 12°55'E). The isopods were collected from samples of the bladderwrack (*Fucus vesiculosus*) on May 2 and 10, 1990. Two females and a male were reared in containers (0.25 l) with brackish water and a small piece of *Fucus*. The females selected for the experiment were in the preparturial stage, having clearly developed oostegite buds. The containers were checked daily during the 10 day period. If precopula was observed ($n = 58$) or if one of the females had a marsupium ($n = 44$), the isopods were removed and their body length (to the nearest 0.5 mm) was measured. We thus assumed that the females with a marsupium had undergone parturial ecdysis and copulated with males. The total material consisted of 102 pairs of females, and each male was used only once. The colouration of the females was determined on the basis of their darkness, the degree of albafusca pattern and the number of white dorsal lines (i.e. morphs *lineata*, *bilineata*, *trilineata*; see Salemaa 1978 on the colour polymorphism of *I. balthica*, and Jormalainen & Tuomi 1989 on the classification of the morphs).

2.3. Pairing in experimental pools

The experiments for mate-selection in artificial populations were carried out at the Archipelago Research Institute in SW Finland (60°14′N, 21°60′E). The isopods were collected from the vicinity of the Institute in late May and early June 1989. Within a week the animals were divided into four experimental 60 litre pools. In each pool we constructed a habitat consisting of stones with epiphytic green algae (*Cladophora* spp.) and two to three clumps of bladderwrack (*Fucus vesiculosus*). The pools were located outside and shaded from direct sunlight, and they had a continuous throughflow of brackish water.

The experiments in three pools were started on June 3 and the fourth one on June 7. At the start of the experiment the body length of the isopods was measured (mm) from the front edge of the head capsule to the back edge of the telson, and the reproductive condition of females was determined on the basis of the oostegite buds or plates (Haahtela 1978). In two of the pools the sex ratio of the animals was manipulated to 30 females and 60 males, and reversed in the other two, i.e. 60 females to 30 males.

The pools were checked once after two to five days from the start. The precopulatory pairs were removed from the pools, and the length of the paired animals and the reproductive condition of females were checked. The rest of the isopods were allowed to form pairs for another seven to eleven days, after which the experiment was stopped. At the end both the paired and the unpaired animals were measured, and their colouration and reproductive condition were observed.

3. Results

3.1. Male choice of female characteristics

The present experimental design allowed a male to choose between two females which on average differed 1.5 mm ($SD = 0.7$, $n = 102$) in length. Males were on average 5.4 mm ($SD = 1.7$, $n = 102$) larger than the larger females.

We considered that the male had selected the female whom he was guarding or which had undergone ecdysis and had a fully developed marsupium. Later (May 16), when we checked 45 such females, 30 of them were gravid with eggs at the earliest developmental stages (A–B, after Holdich 1968), and their mean brood size was 35.3 ($SD = 19.9$, $n = 30$).

In 71% of all the cases males preferred the larger female over the smaller one. This preference was statistically significant in experiments made on both May 2 when the larger female was selected in 68% of the cases (sign test $P < 0.01$, $n = 57$), and on May 10 when the larger female was selected in 73% of the cases (sign test $P < 0.01$, $n = 45$). The trend was the same among females in precopula (sign test $P < 0.01$, $n = 58$) and among the ones that had undergone ecdysis and had a fully developed marsupium (sign test $P < 0.01$, $n = 44$). In both groups, the larger female was more frequently selected (69% and 73% respectively) and the size selections in the two groups did not differ from each other ($\chi^2 = 0.171$, $df = 1$, $P = 0.679$).

In the entire material, the size difference between the larger and smaller females varied from 0.5 to 3.0 mm. The amount of size difference clearly affected the preference of the males (Fig. 1): The difference in length of the two females was greater in cases where the larger one was chosen (mean difference = 1.65, *SD* = 0.66) compared to cases where the smaller one was chosen (mean difference = 1.22, *SD* = 0.64; $t = 3.027$, $df = 100$, $P < 0.01$). A size difference of 1.0 mm was sufficient to increase the probability over 0.5, and with size differences of over 2 mm the male most pronouncedly preferred the larger female (Fig. 1).

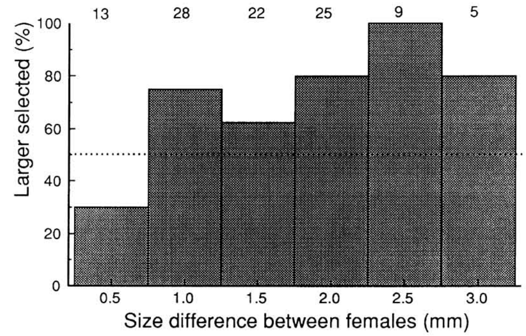

Fig. 1. Frequency (%) of cases where the male selected the larger female for precopula. The data was grouped by the size differences (larger-smaller) between the females. The total number of cases (n) is given for the different groups.

Neither female colouration (Table 1) nor male size affected the probability whether the male selected the smaller or larger female. The mean size of the males was 16.5 mm (*SD* = 1.4, *n* = 72) for those that selected the larger female, and 16.1 mm (*SD* = 1.5, *n* = 30) for those that selected the smaller female. The difference was not statistically significant ($t = 1.540$, $df = 100$, $P = 0.127$). However, we had only a few ($n = 10$) small males (< 15 mm) and a few ($n = 10$) large males (> 18 mm) so that the present material may be insufficient for identifying the overall effects of male size on female-male interactions.

Table 1. The distribution of 100 female pairs depending on the colouration differences between larger and smaller females, and the preference of the male. The G test tests whether the colouration differences affect the preference of the male.

Trait Selected female	The trait expressed in larger female			Test statistics		
	less	equal	more	G	*df*	*P*
Darkness						
Larger	32	16	23			
Smaller	8	4	17	5.83	2	0.054
Albafusca pattern						
Larger	16	40	15			
Smaller	5	14	10	1.92	2	0.383
Lineata pattern						
Larger	7	50	14			
Smaller	5	23	1	5.81	2	0.055

3.2. Mate choice in experimental populations

At the beginning of the experiment the mean body length in different pools varied from 20.0 to 22.0 mm in males and from 15.2 to 17.5 mm in females. The male mortality during the experiment averaged 16% and the female mortality 19%.

The number of precopulatory pairs observed in different pools varied from 7 to 21. 86% of the females found in precopula had clearly developed oostegite buds, their next moult being the parturial one. At the end of the experiment 60% of the solitary females had eggs in their marsupium, and we considered these females as having paired and copulated during the experiment. The rest of the solitary females were either in the stage before the parturial moult (20%) or had undergone the parturial ecdysis but had no eggs in their marsupium (20%).

The size differences between solitary and paired animals were analyzed by considering one pool as an independent replicate and the mean sizes of solitary or paired isopods as paired measures. When comparing the size distribution

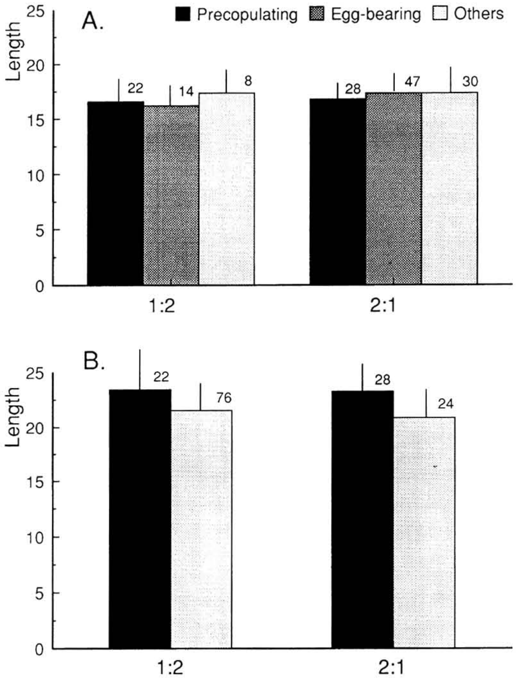

Fig. 2. The mean length of paired and unpaired females (A) and males (B) in the artificial pool populations in two sex ratios (females:males) with standard deviations and n:s at the top of the bars.

of paired and solitary females (Fig. 2A) there were no differences, and the result was the same whether (Two-way ANOVA for paired comparisons: *df* = 1, 3; *F* = 1.07; *P* = 0.378) or not (Two-way ANOVA for paired comparisons: *df* = 1, 3; *F* = 1.44; *P* = 0.316) the solitary females with eggs were included in the group of paired females. The guarding males, however, were clearly larger (Two-way ANOVA for paired comparisons: *df* = 1, 3; *F* = 11.78; *P* = 0.042) than the solitary ones (Fig. 2B), and the trend was the same in both the sex ratios used (Fig. 2B).

The correlation of the male and female lengths within precopula-pairs was not significant in either sex ratios (females:males; 1:2 sex ratio: $r = 0.32$, $n = 23$, $P = 0.132$; 2:1 sex ratio: $r = -0.17$, $n = 28$, $P = 0.394$). Thus the pair formation was not size-assortative.

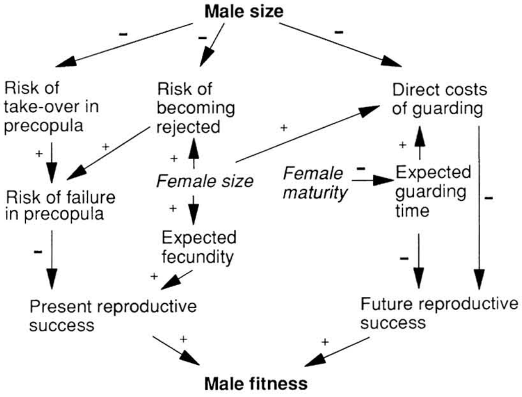

Fig. 3. Some hypothetical relationships that can modify male fitness as a function of male and female body size in species in which the male is guarding the female during a precopulatory period. The + and — signs indicate the suggested direction of the association between the two variables. The schema assumes that 1) large male size is beneficial in both intra- and intersexual interactions, and 2) both female size and maturity can function as potential criteria of mate choice for males.

4. Discussion

The males were clearly able to discriminate between different sized females when given a choice of a small and a large female, and the choice was evident even for a 1.0 mm difference in female length. The male's preference for large females is also observed in *Asellus* (Manning 1975), some *Jaera*-species (Veuille 1980, see also Veuille 1986), *Thermosphaeroma* (Shuster 1981) and gammarids (Elwood et al. 1987, Dick & Elwood 1989) and is generally explained by the positive correlation of brood size and female size (e.g. Ridley & Thompson 1985; Fig. 3). Such positive correlations are also found in *I. balthica* (Romanova 1974, Salemaa 1979). A male selecting a large female would obviously gain in fitness, if the females were otherwise equal.

We cannot, however, exclude the possibility that the criteria by which the male makes the guarding decision may be some size correlated trait rather than the size itself. For instance, males may be able to test the maturity or the stage of the moulting cycle of the female, and select a female that matures sooner for parturial ecdysis, as observed in *Gammarus* spp. (Dunham et al. 1986, Dick & Elwood 1989) and some isopod species (Shuster 1981, Thompson & Manning 1981; Fig. 3). By doing this a male can minimize the guarding time and the associated costs of breeding. By minimizing guarding time he can maximize the number of copulations presupposing there are acceptable females available. A guarding decision may therefore be sensitive to sex ratio (Ridley & Thompson 1985) or the male's experiences concerning available females (Dunham & Hursham 1990). The costs of guarding may include energy costs caused by carrying a passive female (Adams & Greenwood 1983; direct costs, Fig. 3) and increased predation risk (Ward 1986, but see also Verrel 1985 for opposite; indirect cost).

Although the males clearly showed discriminatory behaviour on female size or some correlated trait when given a choice of two females the male choice of size was not apparent in experimental populations. The complex habitat used in the pools offers hiding places for females, thereby probably reducing the probability of the male meeting and comparing female candidates. This may have affected the male's assessment processes behind the guarding decision (Dick & Elwood 1989) due to the male's insufficient information on the female population, and may be particularly true if the males have an adjustable threshold for guarding decisions. Dunham & Hursham (1990) manipulated the experiences of *Gammarus lawrencianus* males before a mating decision by keeping them with or without a female, and observed that males without former female experiences proceeded to precopula more eagerly than experienced males. A 10 day isolation was enough to change the male's mating decision. With this model the male's selectivity should vary with the probability of meeting female candidates. A complex habitat and also the presence of other males may both be factors affecting a male's guarding decision.

The selection for larger females would be most likely to occur when the sex ratio is female biased. However, in the spring the situation in *I. balthica* is the reverse (e.g. Salemaa 1979, Jormalainen & Tuomi 1989). In such cases, there is a high risk that the male will not find a female at all, and the male may thus readily select any female, if she is mature for breeding. The size of the female can only be the second choice.

The males found in precopula were larger than the solitary ones. This assumes either that the larger males form pairs more eagerly than the smaller ones or generally guard females for longer times than smaller males (as in *Gammarus pulex*; Elwood & Dick 1990), or that the success of precopula depends positively on size (Fig. 3). At present we have no evidence for a differential pairing tendency or duration of precopula among the different sized males. In the laboratory experiment, male size did not affect the probability whether the male selected the smaller or larger female. Direct male-male conflicts can be observed in the laboratory when solitary males attack precopulatory pairs, and we have also witnessed take-overs. Thus the differential pairing success of different sized males at least partly results from male-male competition. If, however, the male-male competition were the only explanation, the size difference between precopulatory and solitary males should vary with the intensity of competition. When the sex ratio is strongly female biased we do not expect as large size differences as when the sex ratio is more male biased. The sex ratio had no effect on the sizes of precopulatory males in our experimental populations.

The larger size of precopulatory males may also be partly attributable to female resistance. Females seized in precopula are often seen actively resisting and trying to escape by writhing jerkily so that relatively small males seemingly have difficulties in holding the female. By resisting, the female could test the size and/or condition of the partner and make a choice.

To conclude, we suggest that the male choice for female size has a potential role in sexual selection in *I. balthica*. We suspect, however, that female maturity may, in fact, be a more crucial trait for male fitness, and that environmental heterogeneity tends to confound the effects of female size. Intrasexual competition may favour large male size, but at present we cannot exclude the possibility that female behaviour may also lead to non-random pairing with respect to male size.

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