



# Dynamics of intersexual conflict over precopulatory mate guarding in two populations of the isopod *Idotea baltica*

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Aggressiveness during intersexual conflicts is predicted to depend on its costs, the value of winning and the power asymmetry of the contestants, all of which may vary between populations. In the marine isopod *Idotea baltica* (Pallas) a conflict occurs as females resist the attempts by males to start precopulatory mate guarding. We analysed contest dynamics with respect to female maturity stage, that is, to time left to reproductive moult, with which the payoffs of guarding for males and females change. We did this in two populations that differ in synchrony of reproduction, sex ratio and the degree of sexual dimorphism. The intensity and dynamics of contests differed between populations: in the more size-dimorphic population, females, the smaller sex, resisted less by forceful flexing but more by hooking their body than in the other population. Male aggressiveness stayed at a constant level with respect to female maturity. In the less size-dimorphic population, female resistance by flexing was intense and it decreased, while male persistence increased, with the approaching reproductive moult. Contests were more intense with small than with large males. These results fit well with the predictions from models of conflict behaviour. Assessment of the payoffs of winning versus contest costs, coadaptation of the level of aggressiveness to the other traits affecting contest outcome, and counteradaptations by the sexes to each other largely explain the dynamics and between-population differences of these contests.

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Intersexual conflicts arise when the reproductive strategy of one sex imposes a cost on the fitness of the other sex (Parker 1979; Alexander et al. 1997). Such conflicts are expected to be common because of basic sexual differences, such as investment in gametes and differential reproductive rates, which select for different male and female mating strategies (Trivers 1972; Clutton-Brock & Parker 1992; Arnold & Duvall 1994). These evolutionary conflicts may sometimes lead to aggressive contests between males and females. For example, a typical conflict situation occurs when males attempt to mate and females resist these attempts (Parker 1979). Theoretical models predict that low fitness costs of fighting and high value of winning should increase aggressiveness (Parker 1979; Enquist & Leimar 1987; Clutton-Brock & Parker

1995; Härdling et al. 1999). Owing to the potential costs of contests, individuals are expected to evolve means to evaluate each other's fighting powers and adjust levels of aggressiveness accordingly (Parker 1974a; Enquist & Leimar 1983; Yamamura & Jormalainen 1996; Beaugrand 1997; Hack et al. 1997; Payne & Pagel 1997). Furthermore, the traits affecting conflict outcome are expected to coevolve in an arms race between the sexes (e.g. Parker 1979; Andersen 1997; Brown et al. 1997; Rice & Holland 1997) leading to mutual adaptation of each sex's contest traits.

Precopulatory mate guarding in aquatic crustaceans with time-limited opportunity for fertilization represents one case of intersexual conflict where contests are often found (reviewed by Jormalainen 1998). Conflict over guarding duration arises when guarding is a beneficial competitive strategy for males, but incurs some cost for females, for example, in terms of decreased resources available for reproduction or increased predation risk (Parker 1974b, 1979; Jormalainen et al. 1994). Therefore, females may resist guarding while males are expected to be persistent in their guarding attempts. Where such

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conflict occurs, pair formation will be determined by the result of a contest, that is, the level of investment in aggressiveness of the male and female.

Contest characteristics may diverge between populations for two main reasons. First, the conditions determining the payoffs of winning the contest, for example operational sex ratio or duration of breeding period, may differ between populations. Second, the fitness costs of aggressive behaviour and the chances of winning the conflict are often influenced by other nonbehavioural traits, such as size or secondary sexual structures. Thus, investment in contest behaviour should coevolve with these other characters that affect contest outcome. If populations differ in these characters or, alternatively, in conditions that affect the value of winning, differences between populations in contest behaviour are expected.

Here we examine the temporal dynamics of contests over the start of mate guarding in two populations of the marine isopod *Idotea baltica* (Pallas). These populations are known to differ in adult sex ratio, synchrony of reproduction and the degree of sexual size dimorphism (Jormalainen & Tuomi 1989a, b; Kroer 1989). Adult sex ratio and synchrony of reproduction both influence the intensity of mating competition among males and thus the payoff of mate guarding. Size dimorphism is one determinant of the degree of asymmetry in competitive ability, hereafter power asymmetry, between the sexes. Consequently, all these factors may be expected to affect contest behaviour in these populations. We quantified the aggressive behaviour of both sexes and analysed the probability of pair formation with respect to the stage of female maturity, with which the payoffs of winning change. The value of a female for a male is expected to increase and the cost of guarding for a female to decrease as the female approaches her reproductive moult. To test whether female resistance selects for male size, we also examined the effects of male size on contests and pair formation. Finally, we studied the effect of the male's experience of other individuals on pair formation to see if males can adjust their investment in contest behaviour according to the composition of the mating population.

## METHODS

### Reproductive Biology and Sexual Conflict

Mating in *I. baltica* starts with mate guarding by males, which lasts from hours to several days, and ends after copulation during the female reproductive moult (Salemaa 1979). The start of guarding is characterized by intersexual contests; typically the male attempts guarding, while the female resists and tries to escape by flexing her body rapidly. The male usually reacts by flexing his body in a series of short, quick movements. During these fights the female may also bend her body in a stiff, concave or convex, hook-like posture, which makes it difficult for the male to hold her. The fight may last for up to 1 h (Jormalainen & Merilaita 1993). The contest ends either in separation of the pair when she escapes or he detaches from her, or in cessation of resistance and pair formation. Copulation occurs during

the reproductive moult, which takes place in two parts: the posterior part of the exoskeleton is shed first and the anterior part some hours later (Borowsky 1987). Eggs are laid into the ventral brood pouch after the reproductive moult and brooded there for 3–4 weeks before the release of juveniles (Salemaa 1979). Breeding in the northern Baltic Sea is highly synchronous, the majority of females entering their first reproductive moult within a week or two in mid-June (Jormalainen & Tuomi 1989a, b). This synchrony breaks down in the southern Baltic Sea, where generations overlap and females carrying newly laid eggs are found predominantly between May and September (Kroer 1989). The sex ratio is male biased in the northern Baltic Sea at the beginning of the mating period, whereas in the southern Baltic Sea it is either equal or female biased (Jormalainen & Tuomi 1989b; Kroer 1989).

### Experimental Set-up

We observed contests and formation of precopulatory pairs in the following experimental set-up, which we carried out with a population from the Finnish Archipelago in the northern Baltic Sea (hereafter 'the northern population') and a population from the Øresund, Denmark in the southern Baltic Sea (hereafter 'the southern population').

We did the experiment on the northern population at the Archipelago Research Institute of the University of Turku (60°14'N, 21°40'E) at the beginning of July 1997. Females ( $N=19$ ) in the intermoult stage preceding their first reproductive moult, which had therefore not reproduced before, were collected from the field and maintained individually in 1-litre containers (with aeration, 15°C, natural light–dark rhythm, and a piece of the brown alga *Fucus vesiculosus* for food and substrate). Randomly assigned to each female were two males (size difference 3–6.5 mm). These males were maintained together in another 1-litre container. Starting the day after their collection, each of these two males was individually presented to the female for 5 min once a day. The male at the first presentation was randomly either the smaller or larger one, and the other male was presented to the female after an interval of ca. 12 h. These presentations continued in the same order until the female completed her reproductive moult. Between presentations, males were kept together so that, excluding the short daily presentations to the female, they experienced each other's presence.

The males were presented to the females in small (0.2-litre) containers to ensure they encountered each other. We recorded the duration of each encounter and the number of male and female flexes. If pair formation occurred during the first 5 min, we observed the pair until 15 min had elapsed, or the pair separated or copulated. In these cases, we determined contest duration as the time between the start of the encounter and the last male or female flex. When pair formation lasted over 15 min, the pair was given a piece of alga for food and substrate and left in the container for 1–2 h after which we checked the persistence of the pair bond and returned the animals to their own containers.

We did the experiment with the southern population at the Helsingør Marine Biological Laboratory (56°05'N, 12°30'E) in July 1997. The experimental set-up was similar to the previous one, but we had an additional treatment for the males: half of the males experienced the presence of another female between the presentations to the focal female, whereas the other half had experience of each other only. Hereafter, these male treatments are called 'female experience' and 'male experience', respectively. The small and large males in the female experience group were maintained in separate containers, each having one randomly chosen female as its partner. The focal females, when collected, had already mated at least once (38 carried their previous brood and six had an empty brood pouch). Within 1–4 days of the start of the observations the majority of females gave birth to these broods. Water temperature (18–19°C) was slightly higher than in the experiment with the northern population corresponding to the temperature difference in the field. During the observations, we recorded the time each female spent in a stiff, dorsally bent posture (hereafter 'back hooking') in addition to other behaviours. This female behaviour was recorded only for the southern population because, although present in the northern population, it was seldom observed. After the experiments, the animals were returned to their original sampling sites.

## Data Analyses

Observations of encounter duration and male and female flexing were grouped with respect to the time left to the female's reproductive moult. We carried out ANOVA, Mann–Whitney *U* or signed-ranks tests on mean values for each female and male, averaged through time, to compare populations and male treatments in the southern population. Large and small males were compared with pairwise statistics. All statistical tests are two tailed. We analysed (*t* test or Wilcoxon signed-ranks test) the proportions of males and females showing aggressiveness during the approaching reproductive moult by using a logistic regression. The probability of pair formation with respect to the time left to the female's reproductive moult, male size, population and male experiences was modelled with logistic regression, the CATMOD procedure in SAS statistical 6.12 package (SAS Institute 1990). Significance tests are based on maximum likelihood estimates ( $\beta$ ). First, a saturated model with all main factors and all their interactions was constructed. The model was reduced term by term starting with the most complex interaction. If the exclusion of a term did not decrease the model fit significantly (based on a likelihood ratio test between the two models), the model was reduced again and this procedure continued until the removal of a term significantly decreased the model fit.

## RESULTS

### Sexual Size Dimorphism

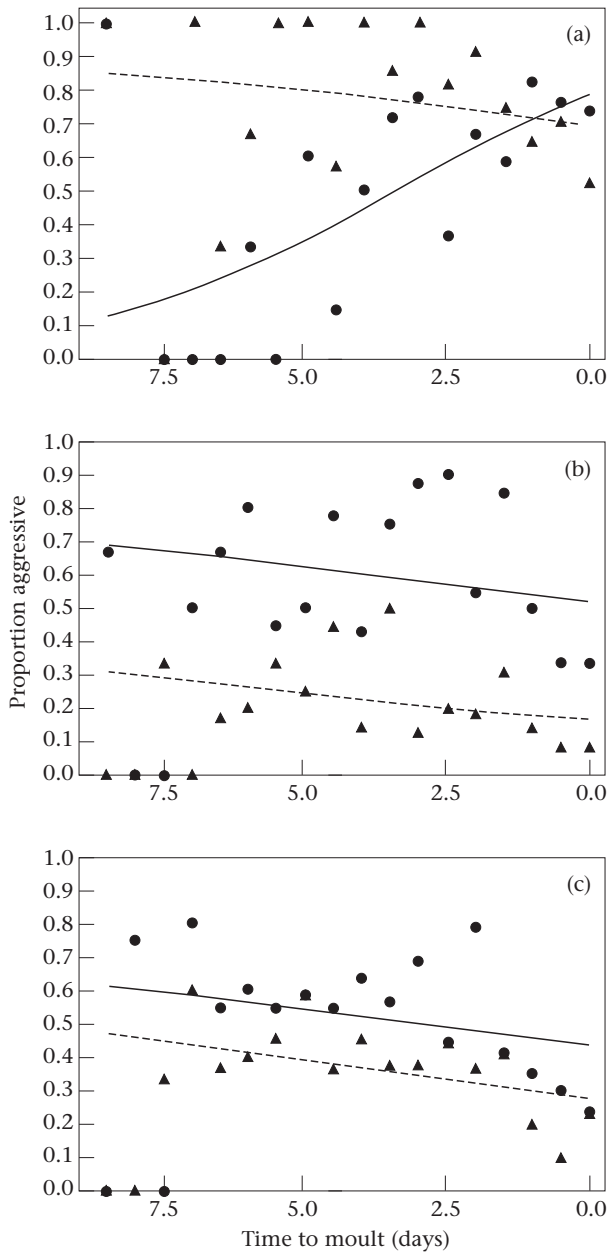
Mature males were larger than mature females in both populations (two-way ANOVA of length, sex:  $F_{1,175}=396$ ,

$P<0.0001$ ), but the degree of sexual size dimorphism varied between the populations (two-way ANOVA: sex\*population interaction:  $F_{1,175}=43.9$ ,  $P<0.0001$ ). Females of the southern population ( $\bar{X} \pm \text{SD}=13.1 \pm 1.57$  mm,  $N=44$ ) were much smaller than those of the northern population ( $17.1 \pm 1.47$  mm,  $N=19$ ). Males, in contrast, were somewhat larger in the southern ( $22.5 \pm 3.01$  mm,  $N=78$ ) than in the northern ( $21.0 \pm 2.34$  mm,  $N=38$ ) population. Consequently, the degree of size dimorphism was much more pronounced in the southern population, where the female length was on average only 58% of the male length compared to 82% in the northern population.

### Contest Dynamics

When contests were analysed as a qualitative trait, that is, flexing either did or did not occur during an observation, logistic regression models revealed differences in the proportion of flexing individuals with respect to time left to reproductive moult between the sexes, between the populations and, in the southern population, between the male experiences. In the northern population, the proportion of males that were aggressive increased with the approaching moult (Fig. 1a; Time:  $\beta=-0.376$ ,  $\chi^2_1=14.3$ ,  $P<0.001$ ), but the proportion of aggressive females remained high without significant changes with time (Fig. 1a; Time:  $\beta=0.11$ ,  $\chi^2_1=1.1$ ,  $P=0.30$ ). The proportion of aggressive males in the southern population decreased slightly with the approaching moult but not significantly so (Fig. 1b, c; Time:  $\beta=0.085$ ,  $\chi^2_1=3.22$ ,  $P=0.07$ ) and there was no difference between the male treatments (Fig. 1b, c; Male experience:  $\beta=-0.167$ ,  $\chi^2_1=2.37$ ,  $P=0.12$ ). The proportion of females fighting also showed a nonsignificant decrease towards the moult (Fig. 1b, c; Time:  $\beta=0.098$ ,  $\chi^2_1=3.63$ ,  $P=0.06$ ). In the male experience treatment, there were significantly fewer females fighting with males than in the female experience treatment (Fig. 1b, c; Male experience:  $\beta=0.343$ ,  $\chi^2_1=7.50$ ,  $P<0.01$ ). When the northern population was compared with the corresponding treatment in the southern population, the temporal trend in the proportion of aggressive males differed significantly between populations (Fig. 1a, b; Time\*Population interaction:  $\beta=0.194$ ,  $\chi^2_1=9.81$ ,  $P<0.01$ ). In females there was no such interaction (Fig. 1a, b; Time\*Population interaction:  $\beta=-0.018$ ,  $\chi^2_1=0.07$ ,  $P=0.794$ ), but the proportion of fighting females was significantly higher in the northern population (Fig. 1a, b; Population:  $\beta=-1.19$ ,  $\chi^2_1=26.1$ ,  $P<0.0001$ ).

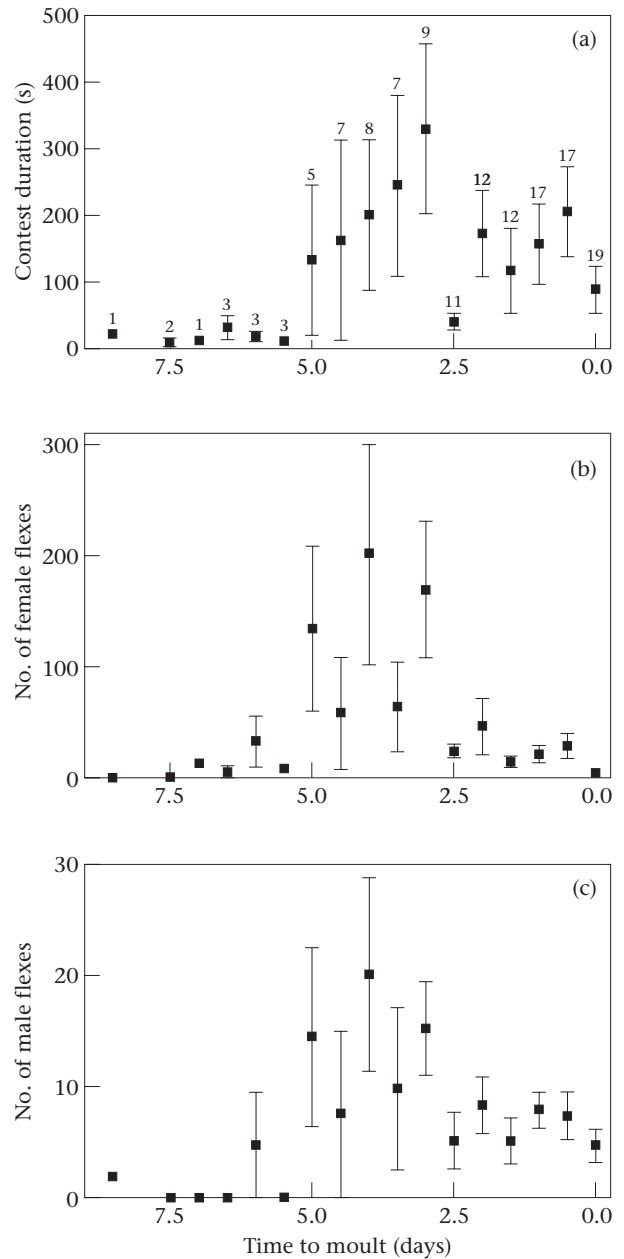
In the northern population, contests were short at the beginning of the experiment, increased in duration around 5 days before the female's reproductive moult and thereafter remained relatively stable (Fig. 2a). Contests were most pronounced 3–5 days before the moult when the total numbers of both female and male flexes peaked (Fig. 2b, c). After the peak, female resistance diminished towards the completion of the moult (Fig. 2b). The intensity of female resistance, measured as number of flexes per unit time, decreased with the time left to moult (correlation:  $r_{135}=0.29$ ,  $P<0.001$ ). In males, the total



**Figure 1.** The proportion of males (●, —) and females (▲, ---) showing aggressiveness (flexing or not) with respect to time left to the female's reproductive moult in the northern population (a) and in the southern population in treatments where males either (b) did not have or (c) had experience of other females between the daily 5-min periods they were with the focal female. Time zero refers to the completion of the moult.

number of flexes decreased (Fig. 2c), but the intensity of flexing, in number of flexes per unit time, increased with the approaching moult (correlation:  $r_{135} = -0.28$ ,  $P < 0.001$ ).

The number of female flexes, averaged through time separately for her large and small male partner, as well as the intensity of female resistance, was higher when the male partner was small (Table 1). Also, the small males flexed more, and with a higher intensity, than the large males (Table 1). However, after the tablewide sequential



**Figure 2.** (a) Encounter duration and the numbers of (b) female and (c) male flexes ( $\bar{x} \pm SE$ ) during encounters in relation to time left to the female's reproductive moult (0 referring to the completion of the moult) in the northern population. *N*s are given in (a).

Bonferroni correction of the risk levels only the intensity of female resistance remained significant. The mean number of flexes of the large males increased with female size, that is, with decreasing size dimorphism ( $r_{19} = 0.51$ ,  $P < 0.05$ ). Although the contests were more intense with the small than the large male, there was no difference in the mean contest duration (Table 1).

Contest behaviour in the southern population differed from that in the northern population in several respects. Because both male treatments in the southern population showed similar trends, the data were combined for comparisons between the populations. Contests started earlier

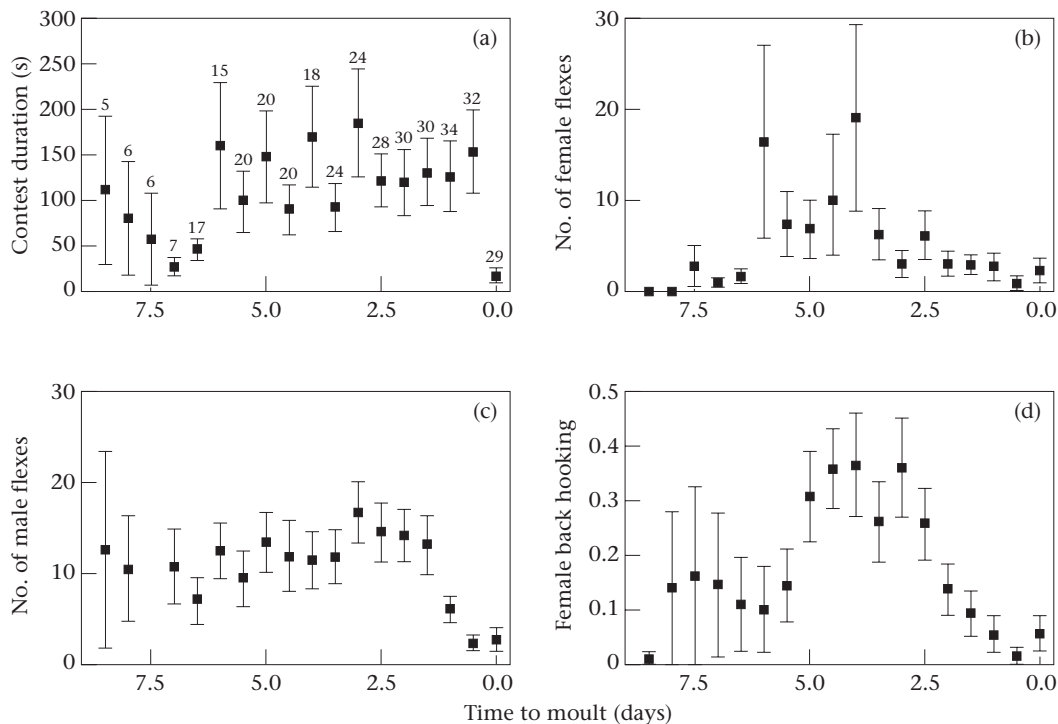
**Table 1.** Contest characteristics ( $\bar{X}\pm\text{SD}$ ; calculated for each of 18 females through time separately for the large and small male) in encounters between females and large or small males in the northern population

Variable	Large male	Small male	<i>t</i>	<i>P</i>
Contest duration (s)	163 ± 175	160 ± 152	0.21	0.830
No. of female flexes	19.1 ± 33.0	56.4 ± 82.1		0.034*
Intensity of female flexes (no./min)	8.04 ± 5.65	18.4 ± 13.7	2.81	0.012†
No. of male flexes	4.65 ± 5.27	10.16 ± 8.63	2.15	0.046
Intensity male flexes (no./min)	2.67 ± 2.43	5.53 ± 5.21	2.19	0.042

Test statistics of pairwise *t* tests, or signed-ranks test for the difference between different-sized males are shown.

\*Signed-ranks test.

†Indicates a significant difference at the tablewide 0.05 risk level after the sequential Bonferroni correction (Rice 1989).



**Figure 3.** (a) Encounter duration and the numbers of (b) female and (c) male flexes and (d) the time female spent back-hooked (as a proportion of total encounter time) during the encounters in relation to time left to the female's reproductive moult in the southern population ( $\bar{X}\pm\text{SE}$ ). *N*s are given in (a).

in the southern population: 8.5 days before the female reproductive moult when the first observations were made (Fig. 3a). Also, the southern population lacked the clear peak around 3 days before the moult observed in the northern population (Figs 2a, 3a). The number of female flexes started to rise 6 days before the moult, but the level of female resistance by flexing was only about a 10th of that of the northern population (Fig. 3b). The mean number of female flexes  $\pm\text{SD}$ , averaged over time, was  $4.68 \pm 5.94$  ( $N=35$ ) in the southern and  $39.3 \pm 50.2$  ( $N=19$ ) in the northern population (ANOVA with log transformation:  $F_{1,53}=31.42$ ,  $P<0.0001$ ). Females also resisted by back hooking, when relatively far from the moult (Fig. 3d). Male flexing remained at a relatively stable level after the start (Fig. 3c). The mean number of male flexes, averaged over time, was higher in the

southern ( $\bar{X}\pm\text{SD}=9.99 \pm 5.68$ ,  $N=35$ ) than in the northern population ( $6.91 \pm 4.80$ ,  $N=19$ ; ANOVA:  $F_{1,53}=4.02$ ,  $P=0.05$ ). There was no correlation between the intensities of female ( $r_{365}=0.09$ ,  $P=0.09$ ) or male ( $r_{365}=-0.02$ ,  $P=0.68$ ) flexing (flexes/min) and the time left to the female's moult in the southern population.

The manipulation of male experience had no significant effect on the mean contest duration, the mean number of male flexes, or the proportion of time females spent back hooking (Table 2). The mean number of female flexes tended to be higher when the male was maintained with another female, but this difference was not significant after the Bonferroni correction for risk levels (Table 2).

We found no differences in any of the mean contest characteristics (contest duration, numbers of male and

**Table 2.** Contest characteristics ( $\bar{X}\pm\text{SD}$ ; calculated for each female over time) in encounters between females and males that had prior experience with either males or females in the southern population

Variable	Male experienced a female	N	Male experienced a male	N	Z/F	P*
Contest duration (s)	116±91	21	115±83	14	Z=0.22	0.83
No. female flexes	6.3±6.9	21	2.2±2.8	14	$F_{1,33}=4.14$	0.05
Time female spent back hooking (%)	16±12	21	13±10	14	$F_{1,33}=0.34$	0.56
No. of male flexes	9.5±5.5	21	10.7±6.0	14	$F_{1,33}=0.37$	0.54

Test statistics of Mann–Whitney *U* tests or ANOVA for the difference between males varying in experiences are shown.

\*None of the *P* values is significant after the sequential Bonferroni correction (Rice 1989) for the tablewide 0.05 risk level.

female flexes, female back hooking, intensity of male and female flexing), averaged over time, between the large and small males in either of the male treatments, or in the pooled data in the southern population (a total of 18 signed-ranks or pairwise *t* tests, all nonsignificant). The lengths of the small and the large male were not correlated with any of the mean contest characteristics. However, the length of the female correlated positively with the mean contest duration with the smaller male ( $r_{31}=0.44$ ,  $P=0.011$ ), but not with the larger one ( $r_{31}=0.19$ ,  $P=0.31$ ).

### Mate Guarding

The probability of pair formation increased with the approaching reproductive moult in both populations (Fig. 4). In the northern population the terms Time left to female moult and Male size were included in the saturated model, but time alone explained satisfactorily the probability of pair formation (Fig. 4a, Table 3).

In the southern population pair formation depended on Time left to moult, Male experience and Male size (Fig. 4b, c, Table 1). The model could not be reduced because the removal of the Time\*Male size\*Male experience interaction from the model significantly decreased the fit of the model ( $\chi^2_1=8.51$ ,  $P<0.01$ ). This interaction implies that the pair formation probability of large males increased more slowly than that of small males when males had experience of another male (Fig. 4b), while this was reversed when males had experience of females (Fig. 4c).

We found no overall differences between the populations in the probability of pair formation (Fig. 4a, b, Table 3), but we found an interaction Time\*Male size\*Population suggesting that the effect of male size on pair formation differed between the populations. Excluding the interaction term significantly decreased the fit of the model ( $\chi^2_1=6.27$ ,  $P<0.05$ ).

We analysed the effect of flexing on the probability of pair formation by entering Time left to moult, Number of male flexes, Number of female flexes and all interactions between these factors as explanatory variables. In the northern population the simplest model fitting the data (likelihood ratio:  $\chi^2_{122}=100$ ,  $P=0.93$ ) included Time left to moult ( $\beta=-1.041$ ,  $\chi^2_1=24.2$ ,  $P<0.0001$ ) and Number of male flexes ( $\beta=0.128$ ,  $\chi^2_1=15.4$ ,  $P<0.001$ ). In the southern population this model (likelihood ratio:  $\chi^2_1=171$ ,  $P=0.93$ )

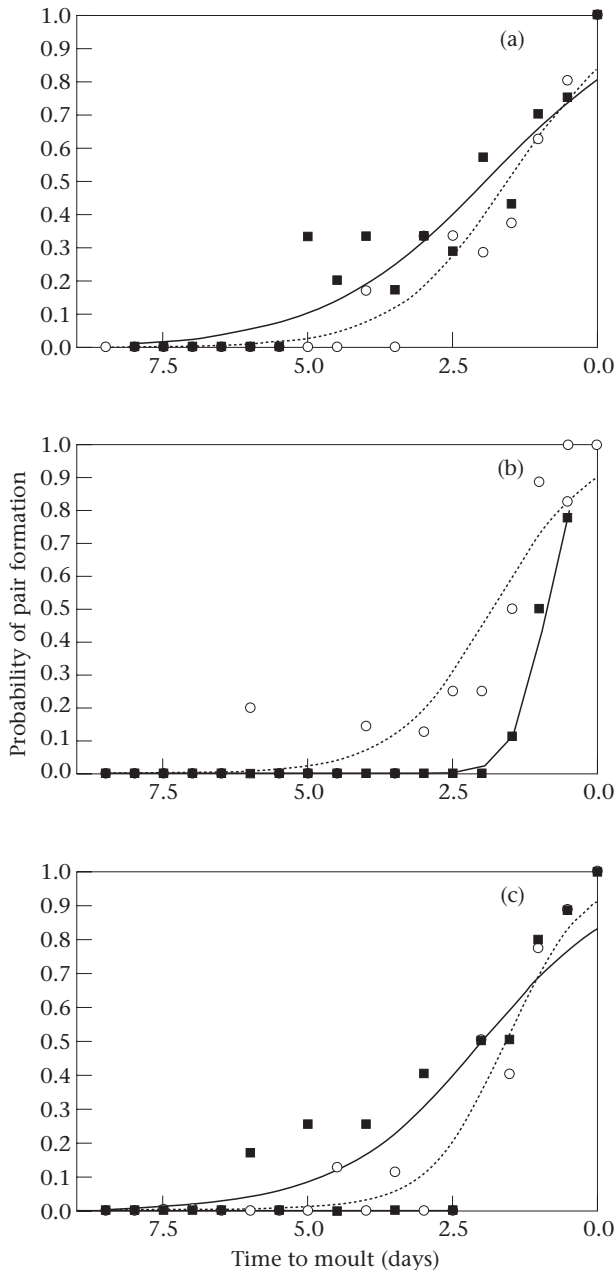
similarly included the Time left to moult ( $\beta=-1.38$ ,  $\chi^2_1=64.2$ ,  $P<0.0001$ ) and the Number of male flexes ( $\beta=-0.03$ ,  $\chi^2_1=2.18$ ,  $P=0.14$ ), but there was also a significant interaction of these two ( $\beta=0.02$ ,  $\chi^2_1=11.4$ ,  $P<0.001$ ) indicating that the effect of male flexing was not constant over time.

## DISCUSSION

### Dynamics of Behavioural Conflict

Contest characteristics of both sexes in the northern population fitted well with the prediction that investment in contests should be determined by the value of winning: for males the value of a female increases with her maturity because time invested in mating will be shorter and the risk of losing her to another male lower. For females, the costs of guarding are expected to increase with guarding duration. Accordingly, as indicated by the number of flexes during encounters, long before the reproductive moult, males were nonaggressive but almost all females showed at least some aggressiveness. With the approaching moult, males were more frequently aggressive, and the proportion of aggressive females remained high. The level of female resistance, after peaking, clearly decreased with the approaching moult. Furthermore, as expected, the intensity of female resistance decreased, and the intensity of male aggressiveness increased, with the approaching moult.

To understand the male and female levels of aggressiveness it is necessary to consider the natural time sequence in a fight. According to the sequential assessment game (Enquist & Leimar 1983), antagonistic encounters involve a series of steps during which the contestants acquire information about how hard the opponent is likely to fight. This depends on both the opponent's fighting ability and investment in fighting, the latter varying with the value of winning (Enquist & Leimar 1987). The party assessing itself as inferior should retreat as soon as this assessment has been done. Thus the length of a fight should be inversely proportional to differences both in the fighting ability and in the value of winning for the contestants. Several of our results, especially in the northern population, are consistent with the idea that the contestants assess their opponents and adjust fighting accordingly. First, the majority of intense and long-lasting contests were found in the middle of the contest



**Figure 4.** Probability of precopula formation with respect to time left to the female reproductive moult separately for the large (■, —) and small (○, ----) males in the northern population (a), and in the southern population in treatments, where males either (b) did not have or (c) had experience of other females during the daily 5-min periods they were with the focal female.

period when both sexes had relatively more to win. Second, the levels of aggressiveness were lowest when asymmetry in the value of winning for the sexes was largest, that is either far from or close to the reproductive moult. Third, fights were more intense with the small than the large males as expected from the lower power asymmetry. Finally, contests were more intense or more long lasting with decreasing size dimorphism of the contestants in both populations.

### Between-population Differences in Contest Behaviour

The existence of conflict in both our study populations indicates that the optimal guarding duration is longer in males than in females in both populations. In *I. baltica* the potential reproductive rate of males is high compared to that of females which increases male–male competition. Moreover, long guarding duration for males is favoured by a male-biased sex ratio in the northern population and asynchrony of reproduction in the southern population (see Yamamura & Jormalainen 1996 for combined effects of sex ratio and synchrony of reproduction). However, we found clear differences in the dynamics of contests between the populations.

First, females in the southern population resisted much less by flexing than in the northern population. Instead, they resisted more by back hooking. Different resistance strategies are probably coupled to the differences in sexual size dimorphism. Because of the large size difference between the sexes, the small females of the southern population are unlikely to win fights by force and, therefore, back hooking may be a more effective way of resisting.

Second, in the southern population male persistence was almost independent of the time left to the female's moult, while in the northern population persistence clearly increased with the approaching moult. In the southern population males at encounter take the female and start flexing. During the relatively long encounter they assess the female's stage of maturity because they finally detach from her if she is far from her moult. On the other hand, in the northern population encounters with females far from their moult end in a few seconds, without male aggressiveness, suggesting that the male assesses her almost instantly. Thus, at least the duration of the assessment process differs between the populations. Intense female resistance with a clear temporal trend may be the key factor determining the male's decision in the northern population. Intense female resistance long before the reproductive moult may force males to suppress fighting because the cost of escalated fights could soon exceed the value of being able to monopolize the female. The level of female resistance in itself, instead of female maturity, may have become the assessment criterion of the males for choosing their level of persistence.

We thus suggest that the investment of females in these contests has coadapted with size dimorphism, the females of the less power-asymmetric population showing forceful resistance. The persistence criteria of males, and maybe their assessment criteria of female quality, in turn, seem to have counteradapted to these differences in female resistance strategies. The power asymmetry between the sexes, that is, males being larger than females, has been suggested to result from large size being more crucial for reproductive success in males than in females (Merilaita & Jormalainen 2000). The degree of this power asymmetry differed between the populations, northern females being larger than southern females. This may be because, in the north, there is a long, cold

**Table 3.** Maximum likelihood estimates ( $\beta$ ; excluding intercepts) and the goodness-of-fit statistics of the final logistic regression models explaining the probability of precopula formation in the northern and southern populations, and the model with both the northern population and the corresponding male experience group from the southern population

Variation source	$\beta$	$\chi^2_1$	$P$	Likelihood ratio		
				$df$	$\chi^2$	$P$
<b>Northern population</b>				32	11.58	1.000
Time	-0.84	27.66	<0.001			
<b>Southern population</b>				63	45.11	0.957
Time	-1.75	29.85	<0.001			
Male experience	-0.35	0.69	0.406			
Male size	0.03	0.01	0.942			
Time*Male experience	0.58	3.26	0.071			
Time*Male size	-0.38	1.44	0.230			
Male experience*Male size	-0.41	0.99	0.320			
Time*Male size*Male experience	0.74	5.28	0.022			
<b>Both populations</b>				59	20.70	1.000
Time	-1.52	16.25	<0.001			
Population	0.45	0.92	0.337			
Male size	0.33	0.50	0.481			
Time*Population	-0.65	2.95	0.085			
Time*Male size	-0.54	2.08	0.150			
Population*Male size	0.44	0.88	0.347			
Time*Male size*Population	-0.71	3.50	0.062			

The first statistic tests the significance of each term in the final model and the likelihood ratio tests the deviance of the final model from the saturated model. For visualization of the models, see Fig. 4a for the first model, 4b, c for the second model and 4a, b for the third.

growing period before the short reproductive season, which may prevent maturation of females when they are small.

### Contest and Pair Formation

Modelling the probability of pair formation as a function of contest behaviour gives interesting insights into the consequences of fighting. First, male aggressiveness was important in explaining pair formation in both populations. This does not diminish the importance of female resistance; experimental evidence on isopods shows that female resistance is crucial for pair formation (Jormalainen & Merilaita 1995; Jormalainen & Shuster 1998). The result emphasizes that the level of male aggressiveness is important in overcoming female resistance and, thus, female resistance is likely to select for aggressiveness in males. Second, the effect of male aggressiveness on pair formation differed between the populations. In the northern population the probability of pair formation increased continuously with male aggressiveness. In the southern population there was no constant positive effect of male aggressiveness on the probability of pair formation. These differences imply that the intensity of sexual selection through female resistance on male aggressiveness may vary between populations, being less intense in the south.

The manipulation of males' experience of other individuals affected their guarding behaviour. Because the benefit of mate guarding for males is expected to increase with the number of competing males (Grafen & Ridley

1983; Yamamura 1987), we expected them to try to start guarding earlier when there was a competing male present. Instead, we found a size-specific change in guarding duration. Large males formed pairs closer to the female moult than small males when they had been maintained with another male, while this was reversed when males had been maintained with another female. In our experiment, male experience was not randomized with respect to size, but the large and small males always experienced each other. Therefore, large males may have assessed themselves as competitively superior, trusted their ability to get a mate by taking over a female, and postponed the start of guarding (see also Grafen & Ridley 1983). The large males postponed guarding only in the southern population where the size variation in males is higher because of overlapping generations. Such differences in behaviour between males with differing experience and between populations suggest that males are able to obtain information on the mating environment, that is, sex ratio or availability of mates, and to adjust their behaviour accordingly.

To conclude, the conflict over the establishment of pairing differed between populations. This suggests that contest traits have coadapted with other population characteristics and that intersexual selection may vary between populations. Assessment of the payoffs of winning versus contest costs, coadaptation of the level of aggressiveness with other traits affecting contest outcome, and counteradaptations by the sexes on each other's traits all seem to be factors relevant in explaining the dynamics of mating contests.

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