

Costs of intersexual conflict in the isopod *Idotea baltica*

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Abstract

In sexual reproduction one sex can increase its reproductive success at the cost of the other, a situation known as intersexual conflict. In the marine isopod *Idotea baltica*, males guard females before copulation. The guarding phase is preceded by struggles as females resist males' attempts to initiate guarding. We determined whether the struggle and/or mate-guarding result in fitness costs in the form of decreasing fecundity and lower levels of the energy storage compounds, glycogen and lipids. Females that underwent the period of struggles with males had decreased glycogen levels compared with females maintained alone. No such cost was found for males. Females guarded by a male also had smaller eggs than females that were not guarded. Thus the intersexual conflict, imposed by the fitness maximization strategy of the males, gave rise to both a fecundity cost and an energetic cost for females. The fecundity cost confirms the existence of intersexual conflict in *I. baltica*. This cost is shared by males, suggesting that the intersexual conflict restrains the reproductive output of both sexes.

Introduction

Natural selection favours reproductive strategies that maximize fitness. Because of fundamental differences between the sexes, such as anisogamy, these strategies evolve sex-specifically. A trait or a behaviour optimizing the reproductive strategy of one sex may therefore impose a fitness cost to the other sex, causing a situation referred as intersexual conflict (Parker, 1979). Fitness cost arises for example when one sex loses control over a reproductive decision to the other sex against its own interest. The existence of such a fitness cost is an essential feature of an intersexual conflict, as it constrains fitness maximization of the sexes, thus making the conflict a potential selective agent. Intersexual conflicts over various reproductive decisions are supposed to be extremely common (reviews by Alexander *et al.*, 1997; Brown *et al.*, 1997; Jormalainen, 1998; Arnqvist & Nilsson, 2000) suggest-

ing that their costs may have broad importance in the evolution of mating systems. Nevertheless there are only few studies that have been able to empirically demonstrate the evolutionary potential of conflicts by providing evidence for the existence of fitness costs (see references below).

Mating behaviour is costly in general (Magnhagen, 1991; Watson & Lighton, 1994; Yuval *et al.*, 1994; Otronen, 1995; Polis *et al.*, 1998). Mating costs are important for the evolution of the reproductive strategy of a sex, but do not necessarily affect the fitness of the opposite sex. However, when the costs are the result of the behaviour of the mating partner, for example antagonistic behaviour of the sexes towards each other, they may function as a selective agent for the reproductive behaviours or traits of both sexes. Examples of this kind of mating costs are survival and fecundity costs for females in fruit flies, imposed by male traits that are beneficial in sperm competition (Chapman *et al.*, 1995; Rice, 1996; Tatar & Promislow, 1997), energetic costs for female water striders due to carrying a guarding male (Rowe *et al.*, 1994; Watson *et al.*, 1998), and fecundity costs as a result of harassment by males in a heteropteran bug (McLain & Pratt, 1999).

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The expected response to mating costs caused by the opposite sex is the evolution of counterstrategies, such as resistance to mating attempts (Parker, 1979). Although investment in counterstrategies reduces conflict costs, the counterstrategies themselves are often costly (e.g. Amano & Hayashi, 1998; Härdling *et al.*, 1999). Consequently, sexual conflict is predicted to always lead to decreased fitness (Lewis, 1987; Clutton-Brock & Parker, 1995; Tatar & Promislow, 1997; Härdling, 1999).

Here we quantify the costs of sexual conflict in the marine isopod *I. baltica* (Pallas). In this species, female receptivity to copulation is restricted in time to the reproductive moult; males therefore attempt to monopolize females before actual copulation by guarding them in amplexus (Borowsky, 1987). A conflict occurs when males attempt to start mate-guarding earlier in the female reproductive cycle than the females want to allow it (Jormalainen & Merilaita, 1993, 1995). Thus guarding is preceded by a period of struggle, lasting several days and characterized by guarding attempts by males and resistance by females (Jormalainen & Merilaita, 1993; Jormalainen *et al.*, 2000). At some stage female resistance ceases and the guarding phase, lasting up to 6 days, begins. Guarding ends with the female reproductive moult, during which copulation and immediate oviposition into the ventral marsupium takes place (Borowsky, 1987). We determine whether male–female interactions, i.e. guarding attempts by males, resistance to these attempts by females and actual mate-guarding, impose energetic costs for males and females in terms of their energy storage compounds. In addition, we compare the fecundity of females maintained either alone or together with a male. We show that the male mating strategy is costly for females, and thus the prerequisite for intersexual conflict is present. This conflict also leads to lower reproductive investment, which is a shared fitness cost for both the sexes.

Materials and methods

Quantification of glycogen and lipid reserve

The energetic demands of mating interactions can be met by using stored reserves. The major energy reserves in animals are glycogen and lipids, the former being a quickly accessible resource for fuelling short-term energy-demanding tasks, and the latter a longer-term high-energy storage (e.g. Vinagre & Da Silva, 1992; Wells *et al.*, 1995). Glycogen is a storage compound for sugars; conversion from food sugars to glycogen takes place in hours (Holliday-Hanson *et al.*, 1997). In exercise, glycogen is utilized first, whereas after depletion or while recovering from the task lipids are mobilized (Brooks & Mercier, 1994; Wegener, 1996).

We determined the contents of the two energy reserves by spectrophotometric methods (Van Handel, 1965, 1985, 1995); lipid quantification was determined follow-

ing Van Handel (1985), and glycogen following Van Handel (1995), with the addition of removing the chitin residue before proceeding to glycogen determination. These methods give the amount of glycogen and total lipids in a sample. Determinations were made from dried (24 h at 65 °C) samples. Standard curves for translating absorbency readings were based on three replicate series of known concentrations for both glycogen and lipids, made during the course of the determination procedure. In the lipid determination, in some cases the sample turned brown instead of the normal red during the procedure. These were excluded from the data because the brown colour interfered with the absorbency reading, giving consistently low values.

Dynamics of energy compounds

In order to study the dynamics of the energy compounds under hunger stress, we quantified glycogen and lipid reserves in males and females which were either (1) sampled directly from the field; (2) maintained individually for 6 days in containers with food; (3) maintained for 3 days without food, or (4) maintained for 6 days without food. In treatment (2), the animals were given both *Fucus vesiculosus* (L.), a brown alga which belongs to the natural habitat and food source of *I. baltica*, and artificial aquarium food (shrimp pellets). The experiment was carried out in one-litre containers with a small stone, aeration, a temperature of 13–15 °C, and a natural light rhythm. The animals were collected in the beginning of the breeding season at the end of May in the vicinity of the Archipelago Research Institute of the University of Turku, located in the Finnish Archipelago Sea (60°14' N, 21°40' E), and were assigned randomly to treatments 1–4. The number of replicates varied from 8 to 11 per treatment and sex. At the time of the experiment the females had either just moulted to the intermoult preceding the reproductive moult or were in the previous intermoult stage (cf. Haahtela, 1978). The data from these four treatments were used to explore sexual differences in energy reserves as well as the priority and speed of mobilization of these reserves.

To obtain reference values for the energy compound reserves of free-ranging animals in the field prior to and during reproduction, we collected females that were either at their intermoult stage preceding the reproductive moult or had just moulted and oviposited on 12 and 13 June. The analyses were performed as above, but the eggs of gravid females were dissected and counted and their lipid and glycogen reserve were quantified separately from the female herself.

Effect of intersexual interactions on energy compounds and fecundity

In the main experiment of this study we quantified the effect of intersexual conflict at the levels of energy

compounds and fecundity. Animals for the experiment were collected from the field between 10 April and 5 June, and the sexes were kept separated in the laboratory. When collected, females were at an intermoult stage one or two moults before the reproductive moult. Before they went through the moult preceding the reproductive moult the females were placed individually in 1-L containers. The containers were kept at 15 °C with natural light rhythm and aeration; they had a stone as a habitat and a piece of *F. vesiculosus* and a shrimp pellet as food. Food and water were changed weekly.

As soon as the females moulted to the intermoult preceding the reproductive moult, the experiment was started by assigning the animals to one of the following four treatment groups: (1) A male and a female were maintained together in the same aquarium throughout the intermoult up until the reproductive moult of the female and copulation. These animals experienced both the struggle before the initiation of guarding and the precopulatory guarding phase. Immediately after the female had oviposited, both sexes were analysed for their energy compounds. Eggs were removed from the marsupium and counted, and the egg-mass was dry-weighed and analysed for energy compounds. (2) A male and a female were maintained together from the start of the intermoult until the start of the precopulatory guarding before the reproductive moult. The pair was then separated, and the energy compounds of both sexes were quantified. These animals thus experienced the struggle before the guarding, but not the guarding. (3) An individual, male or female, was maintained alone for the whole duration of the female intermoult. If it was a female, a randomly selected male was given to her at the reproductive moult in order to get her eggs fertilized. When a male was given to a female at the moult, copulation occurred immediately without any contest. After oviposition the female was treated as in group 1. One male from this group was always terminated for analyses when one replicate from group 1 was terminated. (4) A male or a female was maintained alone, but the determination of energy compounds of the female was made before her reproductive moult, at the average time of the start of precopulatory guarding as judged on the basis of group 2. One male and one female in group 4 were always terminated when a replicate from group 2 was terminated.

The animals in groups 3 and 4 function as controls for the costs of intersexual interactions in groups 1 and 2, respectively. Group 1 and the corresponding control group 3 were used to measure the costs of intersexual interactions during the whole intermoult period. Group 2 and its corresponding control group 4 were used to measure the costs of intersexual struggles preceding the guarding phase. Our experimental design of using single animals as controls for male–female pairs was based on our earlier experience of interactions between individuals in 1-L containers; individuals in intrasexual pairs do

not show any direct interactions, whereas individuals in intersexual pairs interact intensely. Competition for food is excluded in this setup by keeping food resources superabundant throughout the experiment.

All the animals were checked twice a day, at approximately 12 h intervals, to record moults, guarding and oviposition. In the statistical analyses, body size was used as a covariate to control size-related variance in energy compounds. We used length rather than weight as a measure of body size, because weight is known to vary depending on the intermoult stage (Strong & Daborn, 1980), and thus is not independent of our treatment group. The fulfilment of the assumptions of ANCOVA – normally distributed error variance, homoscedasticity of variances and equality of the slopes between the dependent variable and the covariate in different treatment groups – was checked before accepting the analysis.

Results

Energy compounds in males and females and the effect of starvation

The constitution of energy compounds differed between the sexes. Males had more glycogen than females (Fig. 1a; two-way ANOVA, effect of sex: $F_{1,67} = 5.87$, $P < 0.05$), and the lipid concentration of females was clearly higher than that of males (Fig. 1b; two-way ANOVA, effect of sex: $F_{1,55} = 20.4$, $P < 0.0001$).

The effects of starvation and laboratory maintenance on the amounts of glycogen and lipids were tested by pairwise contrasts. The starvation effect was tested by contrasting the two starvation groups against the fed group maintained in the laboratory, while the effect of laboratory maintenance was tested by contrasting the laboratory-maintained, fed group with the group analysed immediately after collection from the field. These contrasts were performed only after a significant treatment effect had been detected in a two-way ANOVA (glycogen: $F_{3,67} = 18.0$, $P < 0.001$; lipids: $F_{3,55} = 2.6$, $P = 0.06$), with a nonsignificant treatment*sex interaction (glycogen: $F_{3,67} = 1.49$, $P = 0.22$; lipids: $F_{3,55} = 0.2$, $P = 0.89$). Laboratory maintenance with food decreased the glycogen concentration (Fig. 1a; field vs. fed 6 days: $F_{1,67} = 10.6$, $P < 0.01$), but had only slight if any effect on the lipid concentration (Fig. 1b; field vs. fed 6 days: $F_{1,55} = 3.24$, $P = 0.08$). Starvation for 3 days tended to decrease and starvation for 6 days significantly decreased glycogen concentration (Fig. 1a; fed 6 days vs. starved 3 days: $F_{1,67} = 3.31$, $P = 0.07$; fed 6 days vs. starved 6 days contrast $F_{1,67} = 12.4$, $P < 0.001$). However, starvation had no effect on lipid concentration (Fig. 1b; fed 6 days vs. starved 3 days: $F_{1,55} = 0.08$, $P = 0.77$; fed 6 days vs. starved 6 days: $F_{1,55} = 0.70$, $P = 0.40$). The glycogen concentration after 6 days of starvation had decreased to about 30% of its original value, while the concentration of lipids was still at its original level.

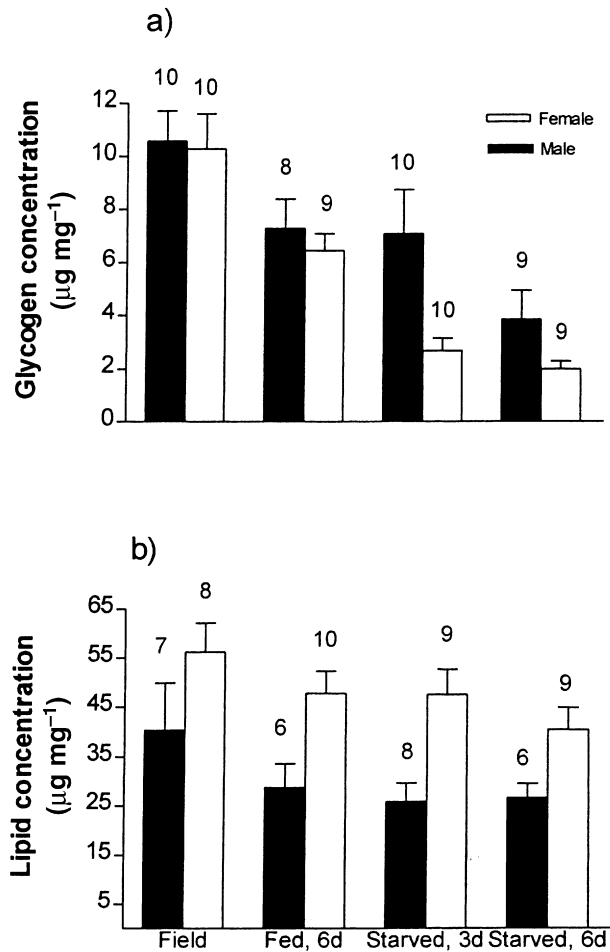


Fig. 1 Glycogen (a) and lipid (b) concentration (mean \pm SE) of males and females collected directly from the field, fed in the laboratory for 6 days, or starved in the laboratory for 3 or 6 days.

Levels of glycogen and lipids in females during the reproductive season

The glycogen reserve of females was at its highest when females were in the early stages of the intermolt interval preceding the reproductive moult (Fig. 2a). It had decreased significantly by the late stage of the same intermolt (Fig. 2a; early – late intermolt contrast: $F_{1,31} = 8.61$, $P < 0.01$), but did not change significantly at the next moult (Fig. 2a; late intermolt – after moult contrast: $F_{1,31} = 1.12$, $P = 0.30$).

The lipid reserve of females was relatively high already in the beginning of the intermolt interval preceding the reproductive moult (Fig. 2b), and it did not change in the late stages of the intermolt (Fig. 2b; early – late intermolt contrast: $F_{1,28} = 0.13$, $P = 0.72$). The somatic lipid reserve of gravid females was only about 60% of the total lipid reserve of females at the preceding intermolt stage (Fig. 2b; intermolt – after moult contrast: $F_{1,28} = 4.48$, $P < 0.05$), because a large part of the lipids

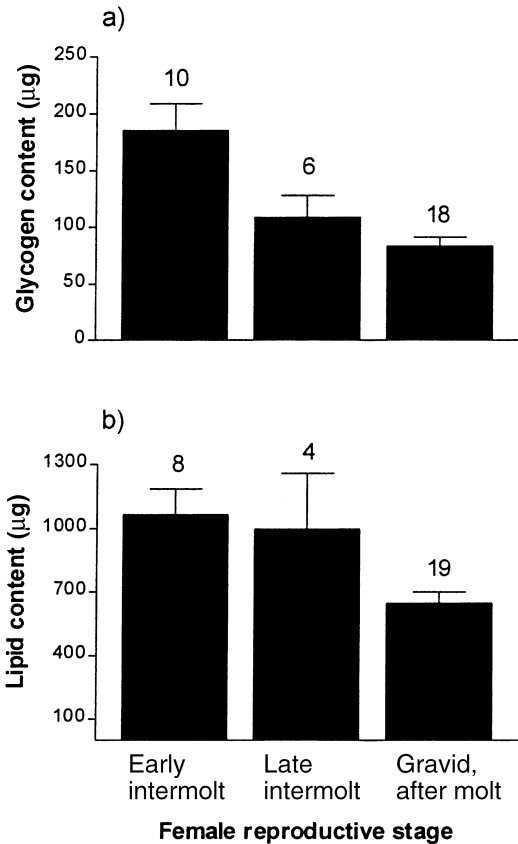


Fig. 2 Glycogen (a) and lipid (b) reserve (mean \pm SE) of females collected from the field at various intermolt stages. Early and late intermolt refer to the point of the intermolt immediately preceding the reproductive moult, after which females become gravid.

Table 1 Egg data collected from the field. All weight measures are dry weights. Single egg weight was calculated from egg-mass weight and egg numbers. Reproductive effort (RE) was calculated as biomass contributed to egg-mass [= egg mass/(egg mass + female mass)].

Variable	Mean	SD	<i>n</i>
Number of eggs	210	64	20
Egg-mass weight (mg)	6.18	1.99	20
Single egg weight (µg)	29.0	2.51	20
RE (%)	24.3	5.94	20
Glycogen reserve (µg)	69.2	30.9	20
Lipid reserve (µg)	538	187	9

in the developing ovaries was now deposited in the eggs (Table 1).

The amounts of glycogen and lipids found in the egg mass matched the difference found in the amounts of these compounds between gravid females and females at the intermolt preceding oviposition (Table 1, Fig. 2). About 45% of the total amount of both glycogen and lipids in gravid females was found in their egg mass.

The mean number of eggs was 210 (Table 1), correlating positively with the female size (female dry-weight – egg number correlation: $r = 0.64$, $n = 20$, $P < 0.01$). The mean reproductive effort in terms of biomass contributed to egg-mass was 24% (Table 1).

Sex differences in mating costs

In males we found no energetic costs of mating, either during the struggle phase or during the period including both struggle and guarding phases. Maintaining males with a female did not affect either their glycogen (Fig. 3a; ANCOVA; male treatment effect: $F_{3,107} = 0.89$, $P = 0.45$; length-covariate: $F_{1,107} = 4.76$, $P < 0.05$) or lipid reserve (Fig. 3b; ANCOVA; male treatment effect: $F_{3,66} = 0.36$, $P = 0.78$; length-covariate: $F_{1,66} = 2.25$, $P = 0.14$). It thus seems that the costs of intersexual interactions in terms of energy compounds are low or absent in males.



Fig. 3 Glycogen (a) and lipid (b) reserve (mean \pm SE) of males maintained either alone or with a female from the beginning of the last female intermolt before the reproductive moult until the start of guarding or until the female moult and oviposition.

In females, on the other hand, differences in energy compounds between treatment groups were evident (Fig. 4). These differences were related partly to reproductive stage (pre-oviposition vs. oviposition) and partly to interaction with males (alone vs. with a male). Glycogen reserves differed significantly between females maintained alone and females together with a male up till the start of guarding (Table 2). The glycogen reserves of females that had been with a male, and hence had undergone the period of struggle, were only about 78% of those of the control females (Fig. 4a), indicating that resistance is costly for females. This estimate included glycogen in the ovaries, because these females were carrying highly developed ovaries. After the reproductive moult and oviposition, however, no difference was found

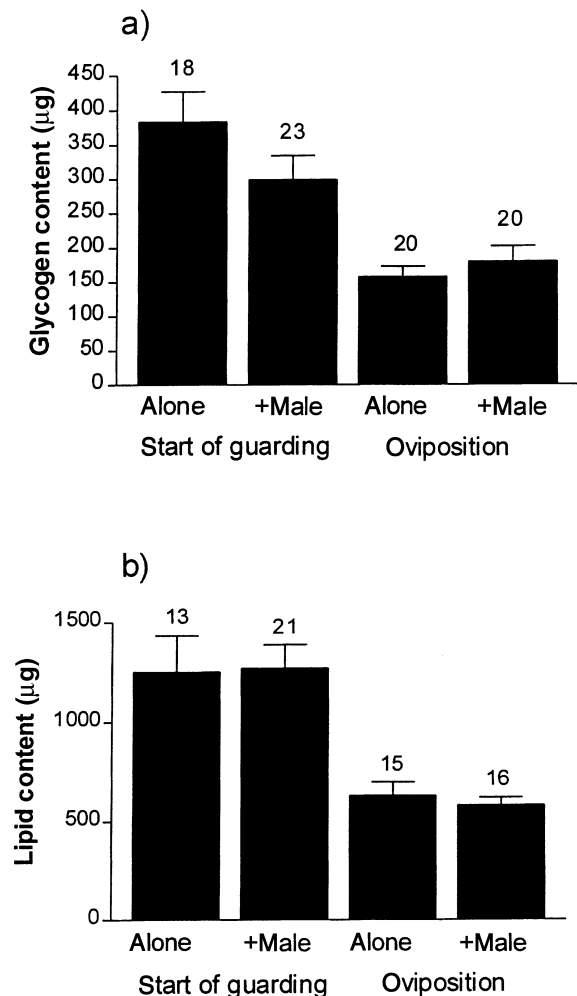


Fig. 4 Glycogen (a) and lipid (b) reserve (mean \pm SE) of females maintained from the beginning of the last intermolt before the reproductive moult, either alone or with a male, until the start of guarding, experiencing only the struggle period or until moult and oviposition, also experiencing guarding.

Table 2 ANOVA table for contrasts between different treatment groups for glycogen and lipid reserve in females. Contrasts were calculated after the significant main effect of female treatment (groups 1, 2, 3 and 4) was found. Data are shown in Fig. 4.

Source of variation	Glycogen reserve			Lipid reserve		
	d.f.	F	P	d.f.	F	P
Alone vs. with a male until start of guarding (group 2 vs. group 4)	176	4.14	<0.05	160	0.01	0.925
Alone vs. with a male until oviposition (group 1 vs. group 3)	176	0.03	0.853	160	0.36	0.552
Alone vs. with a male (groups 3 and 4 vs. groups 1 and 2)	176	1.68	0.199	160	0.13	0.718
Until start of guarding vs. until oviposition (groups 2 and 4 vs. groups 1 and 3)	176	30.5	<0.0001	160	29.5	<0.0001
Covariate: length	176	7.09	<0.01	160	6.31	<0.05

in somatic glycogen reserves between females maintained alone and females with a male (Fig. 4a, Table 2). The overall difference between females before the moult, carrying eggs in their ovaries, and females after the moult, excluding eggs, was significant (Fig. 4a, Table 2) reflecting the considerable amount of glycogen allocated to eggs. Females carrying their ovaries and females which had oviposited also differed in their lipid reserves (Fig. 4b, Table 2), as about half of the total lipid reserve was allocated to eggs. However, we found no effect of intersexual interactions on lipid reserve (Fig. 4b, Table 2).

We found no difference in the number of eggs laid between females maintained alone and with a male (Fig. 5a, Table 3). However, the existence of males had a significant effect on the weight of the egg-mass, as the females maintained with a male laid lighter eggs (Fig. 5b, Table 3). The mean egg weight also tended to be lower, although this was marginally nonsignificant, and reproductive effort in terms of relative egg weight was significantly lower in females maintained with a male than in females maintained alone (Table 3). On the other hand, no differences were found in the glycogen or lipid reserve of the egg-mass between the treatment groups (Table 3).

Discussion

Game theory models of intersexual conflicts assume male and female fitnesses to be mutually interdependent (e.g. Parker, 1979; Yamamura & Higashi, 1992; Clutton-Brock & Parker, 1995; Härdling, 1999). Empirical studies documenting fitness costs arising from acts of the opposite sex are thus crucial in order to demonstrate the existence of sexual conflict and to conceptualize associated behaviours as traits evolved in the context of these conflicts. In the present study with *I. baltica*, we found both a reproductive cost and an energetic cost to females as a result of male mating behaviour. Females that had experienced both the struggle before the

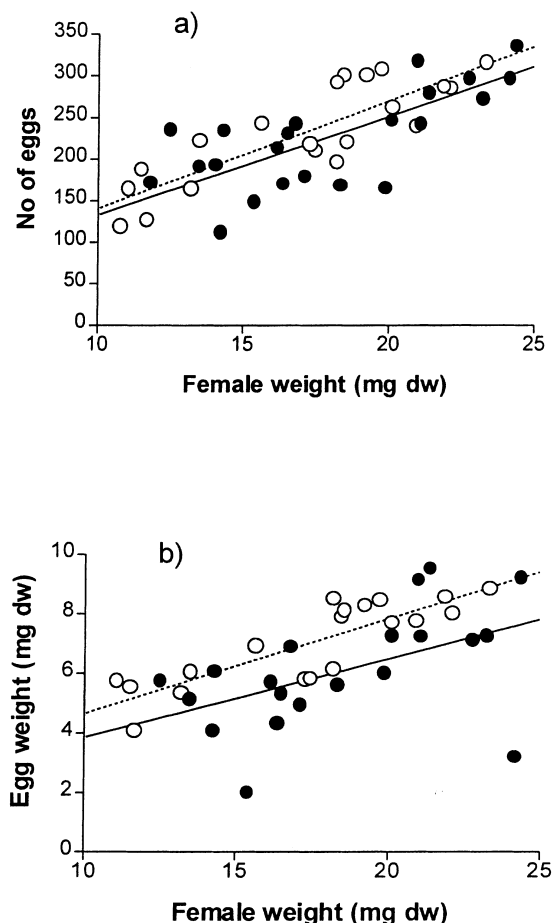


Fig. 5 Number of eggs laid (a) and dry-weight of egg-mass (b) in relation to size of mother in two treatments where females were maintained either alone (open symbols, dotted regression line) or with a male (closed symbols, solid regression line) during the last intermoult before reproductive moult and oviposition.

Table 3 Egg characteristics [mean \pm SD (n)] of females maintained alone or with a male until oviposition, with ANOVA or ANCOVA test statistics comparing differences between female treatments. All weight measures are dry weights. Reproductive effort (RE) was calculated in terms of weights [= egg mass/(egg mass + female weight)].

Variable	Female treatment		Test		
	Alone	With a male	d.f.	F	P
Number of eggs	233 \pm 60 (20)	230 \pm 63 (23)	140	1.75*	NS
Egg-mass weight (mg)	7.03 \pm 1.40 (19)	6.14 \pm 1.91 (21)	137	8.52†	<0.01
Mean egg weight (μ g)	29.8 \pm 2.9 (19)	26.7 \pm 6.4 (21)	138	3.83	0.058
RE (%)	28.8 \pm 2.6 (19)	24.5 \pm 3.3 (21)	138	10.0	<0.01
Glycogen (μ g)	95.6 \pm 38.1 (19)	89.6 \pm 28.1 (19)	135	0.1‡	NS
Lipid (μ g)	529 \pm 94 (12)	485 \pm 126 (15)	124	0.0§	NS

*ANCOVA (mother's weight as a covariate: $F_{1,40} = 64.4$, $P < 0.0001$); †ANCOVA (mother's weight as a covariate: $F_{1,37} = 25.4$, $P < 0.0001$);

‡ANCOVA (egg-mass weight as a covariate: $F_{1,35} = 12.1$, $P < 0.01$); §ANCOVA (egg-mass weight as a covariate: $F_{1,24} = 3.36$, $P = 0.079$).

initiation of mate-guarding and the guarding itself showed a decreased reproductive effort in terms of egg mass. The number of eggs was not affected, as it is determined already at an earlier stage (Sheader, 1977; Jormalainen & Tuomi, 1989), but the eggs were smaller. The type of marsupium found in female *I. baltica* does not allow them to replenish the eggs in any way after ovipositioning (Hoese, 1984). Efficient provisioning of the developing ovaries is therefore a crucial component of fecundity and early embryonal survival for *I. baltica* (Tuomi *et al.*, 1988); lower egg weight translates into smaller size of offspring and most probably also into poorer offspring survival prospects. Decreased fitness payoff from smaller eggs, assuming no equivalent increase in egg numbers, is both theoretically expected (Roff, 1992) and empirically demonstrated by manipulative experiments (Sinervo *et al.*, 1992); low offspring survival from smaller eggs is found in arthropods (Goulden *et al.*, 1987; Fox, 2000) and in fishes (Einum & Fleming 2000). In addition, small size leads to low fecundity in female offspring, as shown here and in other studies (e.g. Shuster, 1991; Sutcliffe, 1993), and to low mating success in male offspring because of both intersexual and intrasexual interactions (Jormalainen *et al.*, 1994; Jormalainen & Merilaita, 1995). Consequently, male mating behaviour carries a fitness cost for females in *I. baltica*. Males share this cost with females because it is expressed in offspring quality. This suggests that the physical conflict (i.e. struggles between males and females before the start of guarding) reflects an intersexual conflict of interests, with the evolutionary potential to shape mating strategies of the sexes in this species.

Females that were with males only before mate-guarding, experiencing the male's attempts to initiate guarding and thus the struggles but not the guarding itself, had decreased glycogen levels compared with females maintained alone at the same time. This demonstrates that interaction with males (or its avoidance) is energetically costly for females during this period. This cost most probably arises from their intense resistance to mating attempts; during a single encounter with a male,

usually lasting a few minutes, the female may forcefully flex her body over 200 times (Jormalainen *et al.*, 2000). Such resistance and the possible avoidance of males may also restrict feeding, thus reducing energy intake. The lipid reserves of females were not affected by the presence of a male. The priority of mobilization of glycogen reserves over lipids was also evident during starvation.

There was no difference in glycogen or lipid levels in the somatic tissue between females that were with a male until the end of the guarding and ovipositioning and females that were maintained alone. The reason for this may be that the glycogen and/or lipid supplies of all females are close to their minimum levels after their resources are exhausted by ovipositioning and moulting, as suggested by the temporal pattern of change in female glycogen and lipid levels.

Our field data on the glycogen levels of females, taken at various reproductive stages, suggest that females pay an even higher cost for resistance in the field. The glycogen reserve of females at the beginning of the intermoult period preceding the reproductive moult was significantly higher than at the late stages of the same intermoult. The sex-ratio estimates in our study population are highly male-biased, and male searching activity is high at the start of the mating period; thus the number of mating attempts may be high (Jormalainen & Tuomi, 1989). The decrease in glycogen levels coincides with the increase in male mating attempts as males begin to be interested in females at the late stage of the intermoult (Jormalainen *et al.*, 2000). Reproductive effort was at the same level and the glycogen reserve was even lower in the field than in females maintained in the laboratory with a male.

Theoretically, the costs of conflict identified here consist of components arising from male mating behaviour (i.e. guarding attempts and guarding) and female resistance, but in the empirical data these components are mixed. The purpose of female resistance is to reduce the costs due to male behaviour, such as restricted feeding, suboptimal diet or increased predation risk (Arnqvist, 1997; Jormalainen, 1998), and it is beneficial

only up to the point where the cost of resistance is outweighed by its benefits (Hårdling *et al.*, 1999). This resistance by females has been shown to be an efficient way to reduce the duration of guarding and thus its costs in *I. baltica* (Jormalainen & Merilaita, 1995).

In contrast to females, we did not find any direct costs arising from struggling or mate-guarding in males. Guarding as such may carry energetic costs for males in mate-guarding crustaceans. However, the eagerness of males to initiate guarding suggests that guarding is often less costly than the alternative, continuing to search for a mate. The costs of guarding for males have been measured in other crustaceans. Robinson & Doyle (1985) found that feeding in males of the amphipod *Gammarus lawrencianus* was restricted during guarding, leading to a lower growth rate. In the isopod *Lirceus fontinalis*, Sparkes *et al.*, 1996) found that the glycogen reserves of males were depleted during the mate-guarding phase. They concluded that guarding is costly for males, and that this cost arises because of restricted feeding opportunities in the refuges where the pairs stay in order to reduce predation risk. Although they did not measure the glycogen levels of females, the suggested mechanism for the source of the cost implies that both sexes face the same cost. Thus a sexual conflict probably occurs in this species too, as indicated by their contest behaviour prior to guarding (Sparkes *et al.*, 2000).

We found a difference in energy storage compounds between males and females. Glycogen levels were higher in males than in females. This may be an adaptation to the more active mating strategy of the males (Jormalainen & Tuomi, 1989). Males search for females and initiate the mating interaction. During the guarding phase they carry the female, and also defend her against take-over attempts by other males (Borowsky, 1987; Jormalainen *et al.*, 1994). As male fitness is generally highly dependent on the number of mates (Trivers, 1972; Arnold & Duval, 1994), fitness maximization in males depends on the capability to repeat the search-struggle-guard-copulate sequence effectively. Such intense and relatively short-term energy-demanding behaviours may be best fuelled by glycogen reserves. Lipid levels, on the other hand, were higher in females than in males. The fitness of a female is not limited by the number of copulations but rather by her investment in offspring numbers and quality (Arnold & Duval, 1994). As female fitness increases with increasing reproductive investment, it may be maximized by the provisioning of energy-rich resources such as lipids for the developing ovaries over a relatively long period (Shaver, 1977). We thus suggest that the sexual differences in the allocation patterns of energy storage compounds can be understood as coadaptations to the general reproductive strategy of each sex.

Game theoretical models on intersexual conflicts predict that the outcome of the conflict depends on the ratio of costs and benefits of winning (Clutton-Brock &

Parker, 1995; Brown *et al.*, 1997). Here we found a cost due to the conflict for *I. baltica* females but not for males. Because of the low potential reproductive rate of females (Borowsky, 1987), and the competition among males for receptive females (Jormalainen *et al.*, 1994), there is an asymmetry in the pay-offs from winning. Thus from the game theoretical point of view, the female winning or losing the struggle over mate-guarding initiation is a matter of the cost of mating; the male is playing for higher stakes, gaining or losing a mating. This suggests a ratio of costs and benefits of winning according to which males should be prepared to invest more than females in the struggles, driving the outcome in the direction of the male optimum and male control of reproductive events. This is supported by the fact that precopulatory mate guarding is the rule in *I. baltica*. However, the resistance by females effectively shortens the guarding time, indicating that the outcome has not reached the male optimum and is not entirely controlled by males (Jormalainen & Merilaita, 1995). The evolutionary potential of this conflict is confirmed by the various adaptation of the sexes to it, such as the guarding posture (*amplexus*) in which the male tries to engage the female, or the temporal adjustment of endurance in guarding initiation attempts by males and resistance by females in relation to the time of female receptivity (Jormalainen *et al.*, 2000).

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