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Intersexual conflict over precopula duration in mate guarding Crustacea

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Abstract

Precopulatory guarding in Crustacea is usually analyzed as a male decision problem. We suggest an alternative possibility that precopula is established as a result of intersexual conflict over precopula duration. Such a conflict can be expected when the male optimum for precopula duration exceeds the female optimum. As a result, males should start precopulatory attempts earlier, while females should resist until close to receptivity. Our analysis reveals two potential sources of conflict: (1) sexual differences in survival probabilities before and during the mate-guarding; and (2) sexual differences in the probability of finding a mate. The latter is perhaps a more probable source of intersexual conflict, since male biased operational sex ratios are common in mate-guarding Crustacea. The former requires that female moulting cycle is synchronous, whereas the latter may operate in populations with asynchronous moulting cycles as well. We further studied the expected intensity of behavioural conflicts in terms of expected present and future fitness gains. In the beginning of the female moulting cycle, there is no conflict. Conflict arises as males start the guarding attempts and females are motivated to resist, and ceases with a decrease in the female's motivation to resist. Several assumptions and predictions of the model are discussed and compared with the behavioural patterns observed in the aquatic isopod *Idotea baltica*.

Key words: Precopula; Mate guarding; Survival; Sex ratio; Sexual conflict

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Introduction

In many aquatic crustaceans (e.g. Isopoda, Gammaroidea) males guard females for some time before the actual copulation (Parker, 1974; Conlan, 1991). This precopulatory guarding behaviour is usually considered as a male competitive strategy which may evolve if the male-male competition for females is strong enough and female receptivity is restricted in time (Parker, 1974), or even if the receptivity is not time-limited but the guarding costs are low enough (Yamamura, 1987). Guarding should be beneficial to the male if the fitness gain achieved by guarding is greater than the expected gain due to continuing search for other females (Parker, 1974). Thus, the rate at which the male encounters females is of fundamental importance. As the encounter rate decreases, duration of the precopula should increase (Parker, 1974). A similar main result arises from the more specific model by Grafen and Ridley (1983; see also Yamamura, 1987, for generalization), and there is supporting empirical evidence from both isopods (Manning, 1980) and gammarids (Dunham and Hurshman, 1990).

Grafen and Ridley (1983) added direct male-male competition into their model on mate guarding by allowing larger males to take over females from smaller males. They predicted that large males have a shorter precopula duration than small males because of the more female biased effective sex ratio of the large males. This result contradicted empirical data (Ridley and Thompson, 1979; Ward, 1984), which led to further modelling by Elwood and Dick (1990). They suggested that the direct guarding costs may affect the duration of guarding, and that such costs are functions of male and female body sizes. Other potentially important variables, thus far not analyzed in the models of mate guarding, may include the strength of female resistance against guarding attempts of males (Grafen and Ridley, 1983, Jormalainen and Merilaita, 1993) or differential predation on precopulatory pairs as compared to single animals (Strong, 1973; Wickler and Seibt, 1981; Ward, 1986).

For instance, the beginning of the precopulatory phase in the isopod *Idotea baltica* is characterized by a period of conflict between the sexes (Jormalainen and Merilaita, 1993). During this period struggles between males and females are frequent as the males continuously attempt to start precopulatory guarding, and the females resist these attempts by kicking and trying to escape. This kind of behaviour seems to be common e.g. in *Gammarus* (Thompson and Moule, 1983; Hunte et al., 1985), in some isopods (Ridley and Thompson, 1979; Shuster, 1981), and in *Artemia salina* (Forbes et al., 1992), but has so far not been analyzed in detail. Jormalainen and Merilaita (1993) proposed two alternative, but not necessarily mutually exclusive, hypotheses to explain the origin of female resistance: (1) the females may resist males in order to perform choices between mate candidates; or (2) the sexes may have different interests concerning the duration of the precopula. The first hypothesis considers female resistance as a female mate choice strategy. The second hypothesis, on the other hand, implies a conflict of interests if females are minimizing the potentially costly time spent in precopula while the males are aiming for longer precopula duration.

These hypotheses, especially the second one, add a new dimension to the existing models of mate guarding, since in most cases the duration of the precopula is considered only as a male decision problem. Below, we make an attempt to identify some factors that can lead to a conflict between the sexes over the duration of the precopula. First, we analyze optimal guarding duration for qualitatively different kinds of gain functions. We emphasize those cases where male and female optima differ. Second, we try to derive

behavioural patterns that may arise from such cases. We suggest two potential sources of conflict, namely, sexual differences in survival probabilities before and during the precopula, and differences in the probability of finding a mate.

Optimal timing of precopulatory guarding

We assume that the female starts her parturial ecdysis at the end of day 1 ($t = 0$), and that females are not receptive to insemination until this moment. There is precopulatory guarding, starting at day $t = t_p$ before ecdysis, and ending in copulation at the start of the ecdysis. Both the male and female are assumed to know the time left to female ecdysis (t). We derive fitness gain functions that include: (i) linear fecundity costs of precopula; (ii) survival before and during the precopula; (iii) the number of matings; and (iv) the probability of finding mates. Conditions for specific optima as well as an ESS analysis of male and female guarding duration in relation to sex ratio are presented in the Appendix.

Fecundity costs

After copulation, the female lays fertilized eggs in her brood pouch, and releases B surviving offspring after the incubation period. The offspring survival, and the survival of the female during the incubation period is independent of the duration of the precopula, but there is a fecundity cost (c), in terms of number of offspring (b), that increases with the duration of the precopula. Biologically this cost may represent e.g. reduced feeding rate or suboptimal diet during the precopulatory guarding.

We use a linear function

$$B(t_p) = b - ct_p \quad (1)$$

where t_p = female maturity at the start of precopula (expressed as days left to parturial ecdysis), c = fecundity cost of the precopula per day, and $b = B(0)$.

When $c > 0$, each day spent in precopula decreases the reproductive gain of both the male and the female. Because of the fecundity cost, other things being equal, both the male and the female have a common interest to minimize the duration of the precopulatory guarding.

Survival costs

We define two survival rates per day, S_1 and S_2 , to both males and females. We start to monitor the survival from day $t = T$ ($t_p < T$). Here T may be interpreted as the duration of one female reproductive cycle equalling one moulting cycle in mature females. $S_1^{T-t_p}$ is survival from day T to the start of the precopula, $S_2^{t_p}$ is survival from the start to the end of the precopula, and the survival over the period T is given by $S_1^{T-t_p}S_2^{t_p}$. When $S_1 > S_2$, the last expression increases as $t_p \rightarrow 0$. When $S_1 < S_2$ the survival over the period T decreases as $t_p \rightarrow 0$.

The fitness gain of one mating can now be written by combining the fertility and survival terms:

$$g(t_p) = S_1^{T-t_p}S_2^{t_p}(b - ct_p) \quad (2)$$

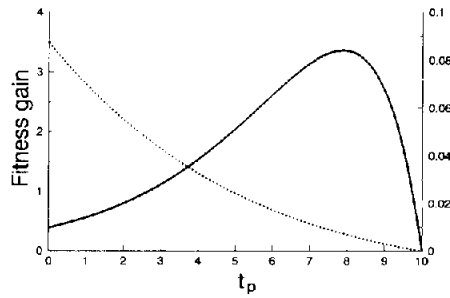


Fig. 1. Fitness gain of the male (solid line, right axis) and the female (dotted line, left axis) according to the equation (2) in relation to precopula duration (t_p) when male survival is assumed to be lower during mate searching ($S_1 = 0.5$) than during the precopula ($S_2 = 0.8$), and the female survival is better before the precopula ($S_1 = 0.9$) than during it ($S_2 = 0.8$). $T = 10$, $b = 10$, $c = 1$.

According to this gain function, the male and female have a common interest in guarding duration if S_1 relative to S_2 is similar (either smaller, equal or larger) for both sexes. However, we can assume either that the behaviour of males during mate search disposes them to greater mortality, or that females have behavioural adaptations to diminish predation risk while being alone, so that (i) for females $S_1 > S_2$, and (ii) for males $S_1 < S_2$.

This difference is interesting because it may imply a conflict of interest between the sexes. In such a case the fitness gains differ between the sexes as a function of time, and the males and females will have different optima for starting the precopula. For example, let $T = 10$, $b = 10$, $c = 1$, and the females have $S_1 = 0.9$ and $S_2 = 0.8$, and the males have $S_1 = 0.5$ and $S_2 = 0.8$. The maximum fitness gain of the female then occurs at $\hat{t}_p = 0$, and the one of the male at around $\hat{t}_p = 8$ (Fig. 1). The shape of the male curve is sensitive to

TABLE 1

Comparison of the optimal duration of the precopula (\hat{t}_p) in cases in which either one mating or repeated mating (two, three or four matings) is allowed according to the equations (A3-4). In all cases $S_2 = 0.9$, $T = 10$, $b = 10$, $c = 1$

One pairing		Repeated pairing			
S_1	$n = 1$	$n = 2$	$n = 3$	$n = 4$	
	\hat{t}_p	\hat{t}_p	\hat{t}_p	\hat{t}_p	
1.0	0	0	0	0	
0.9	0	0	0	0	
0.8	1.5	2.5	2.7	2.8	
0.7	6.0	6.5	6.6	6.6	
0.6	7.5	7.8	7.9	7.9	
0.5	8.3	8.5	8.5	8.5	
0.4	8.8	8.9	8.9	8.9	
0.3	9.1	9.2	9.2	9.2	
0.2	9.3	9.4	9.4	9.4	
0.1	9.5	9.6	9.6	9.6	

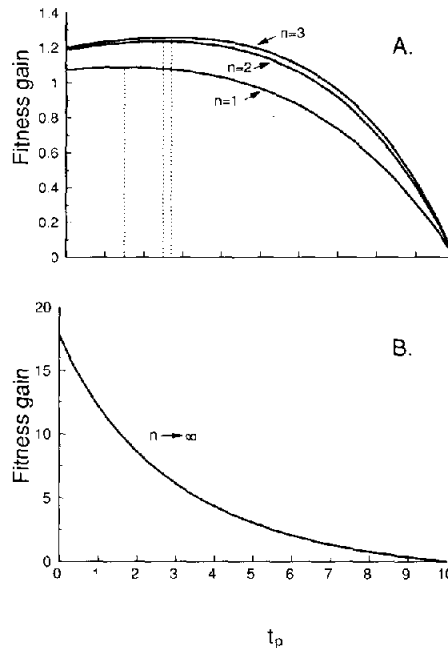


Fig. 2. Fitness gain functions and the optimum precopula durations with different numbers of mates (n) when repeated mating according to equations (A1, A3, A4) (A), or according to equations (A1, A10, A11) (B) is allowed and the survival before the precopula is lower than during the precopula. $S_1 = 0.8$, $S_2 = 0.9$, $T = 10$, $b = 10$, $c = 1$.

survival values, and the values of b and c : $\hat{t}_p > 0$ if S_1 is sufficiently smaller than S_2 (Table 1, Appendix: A6). The optimum \hat{t}_p increases also when the survival condition is fulfilled and the fecundity cost decreases (b increases relative to c ; A9).

From the assumptions (i) and (ii) it follows that: (1) the interest of the female is to start the precopula as late as possible; and (2) the male's fitness gain increases from T to day \hat{t}_p , but after that decreases. Thus we expect that the males would be ready to start the precopula earlier than females.

Repeated mating

In the Appendix, the above analysis is extended to two extreme situations where males are allowed to mate repeatedly. In the first case, the female moulting cycle in the population is exactly synchronous and T is the duration of the female intermoult (A3–4). As a consequence, fitness gain (A1) achieves the maximum at $\hat{t}_p = 0$ if S_1 is high relative to S_2 (A7). However, if S_1 is sufficiently small relative to S_2 (A8), the gain function has an optimum $\hat{t}_p > 0$, and this optimum slightly increases with the number of mates (Fig. 2A, Table 1). As S_1 decreases relative to S_2 the difference in the optimum precopula durations between the cases with different numbers of mates becomes smaller (Table 1).

In the second case, the female moulting cycle is asynchronous and the mean search time per mating is constant (A10–11). In other words, the male has no difficulty in finding a female and he can always pick up any kind of female he wants. Now the male should minimize precopula duration since the fitness gain (A1) is maximized at $\hat{t}_p = 0$ for all S_1

and S_2 values (A12, Fig. 2B). This result is important in two respects. First, the previous condition of intersexual conflict, derived from (2), can be expected to hold only when the female moulting cycle is relatively synchronous. Second, if the moulting cycle is highly asynchronous but precopulatory guarding has still evolved, our assumption of unlimited availability of females is likely to be violated. In fact, Grafen and Ridley (1983) suggested that this is just the case in gammarids. It may well hold also in *I. baltica*. In the northern Baltic, this species is an iteroparous breeder with a well synchronized moulting cycle as almost all females enter the preparturial stage within one week (Salemaa, 1979; Jormalainen and Tuomi, 1989a,b). In the southern Baltic, however, the synchronicity disappears and the population consists of individuals in various moulting stages simultaneously (Kroer, 1989).

Probability of finding mates and sex ratio

We define that males and females find a mate with a probability $P(t)$, and assume that $P(t)$ decreases toward $t = 0$. We use the function

$$P(t) = \left(\frac{t}{T}\right)^z \quad (3)$$

as an arbitrary approximation giving $P(0) = 0$ and $P(T) = 1$. The exponent z defines the form of the $P(t)$ function for $0 < t < T$. Within this area, the smaller is z , the greater is $P(t)$. When $z = 1$, $P(t)$ decreases linearly, and when $z < 1$, $P(t)$ at first decreases slowly but with a continuously steeper slope as t approaches 0 (cf. Yodzis, 1989, p. 306).

The fitness gain function for $t = t_p$ can now be written by combining equations (2) and (3)

$$g(t_p) = P(t_p)S_1^{T-t_p}S_2^{t_p}(b - ct_p) \quad (4)$$

Let us assume similar survival values $S_1 = S_2 = 0.9$, $T = 10$, $b = 10$, $c = 1$, and let z vary (e.g. 0.05, 0.2, 0.4, 1; Fig. 3). The gain function $g(t_p)$ has now a clear maximum

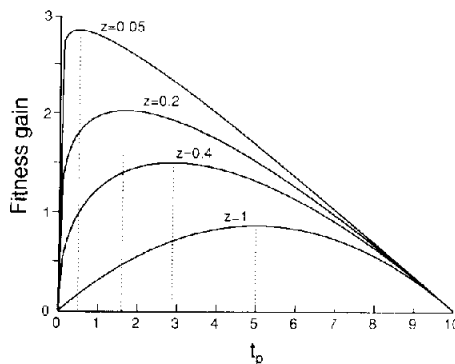


Fig. 3. Fitness gain functions and the optimum precopula durations according to the equation (4) when the probability of finding a mate decreases towards female ecdysis, and the value of z varies. The greater the z value, the lower the probability of finding a mate. $S_1 = S_2 = 0.9$, $T = 10$, $b = 10$, $c = 1$.

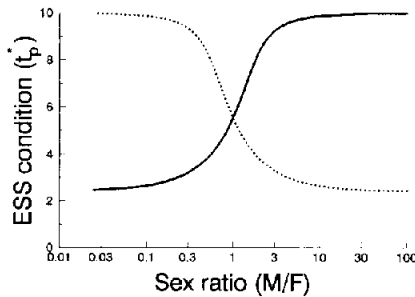


Fig. 4. The ESS condition for guarding duration in males (solid) and females (dotted) in relation to sex ratio. The curves present a numerical solution to equations A25 and A27. $a = 0.001$, $b = 10$, $c = 1$.

point with all z values ($0 < z \leq 1$; A15–16) and the optimal precopula duration \hat{t}_p increases as the z increases (Fig. 3).

The variation of \hat{t}_p with z allows a conflict between the sexes. Specifically, if mature males are more common than mature females, or if the operational sex ratio is male biased, then female can be expected to have a smaller z -value and their optimum precopula duration is shorter than that of males (with all the other variables being equal). This qualitative result is confirmed with an ESS analysis, adopting the approach by Yamamura (1987; see also Yamamura and Tsuji, 1989) and extending it to involve female strategies as well. In the appendix (A17–A27), we derive the ESS conditions for guarding duration for both males and females. As a result, a numerical solution of the ESS conditions (Fig. 4) shows that (1) male guarding duration increases; and (2) female guarding duration decreases as sex ratio becomes more male biased. When the number of males exceeds the number of females the ESS t_p^* for females is always smaller than that of males, and vice versa. Thus, the more common sex should prefer longer guarding time. Note that this result implies a conflict in species in which the male takes the active part in mate search only when sex-ratio is male-biased, and hence males prefer longer precopulas than females. On the other hand, if females are more common, they should prefer longer precopulas than males. However, the latter case will not lead to a conflict if females remain passive during mate search.

Intersexual conflict

Assuming certain fitness gain functions, presented above for males and females, we proceed to analyze the intensity of the behavioural conflict between the male and the female. We first define the “motivation to fight”, and by assuming that the conflict occurs only when both the male and the female are motivated to fight, we derive expected temporal patterns of the intersexual conflict.

Motivation to fight

We assume that the fitness gains associated with the given day t are known by both males and females. Depending on the current and the expected future gains they may begin precopula or try to delay precopula by having the following behavioural options: (1) the female may resist precopula by fighting; or (2) she may accept a guard without a fight;

(3) the male may approach the female and fight in order to take the female by force; or (4) he may give up and detouch the hold; or (5) he may be totally indifferent to females.

Presuming that the individuals are heading to maximal fitness gains by behavioural means the female should be ready to resist precopula attempts of the males when the current gain is low and the expected future gain is high. The male, on the other hand, should be eager to start the precopula when the current gain is high and the expected mean future gain per day is low. Accordingly, we define a measure for female motivation (*FM*) as

$$FM = E[g(t')] - g(t) \tag{5}$$

when its value is positive, and 0 otherwise, and male motivation (*MM*) as

$$MM = g(t) - E[g(t')] \tag{6}$$

when positive and 0 otherwise. Here

$g(t)$ = current fitness gain at day t .

$E[g(t')]$ = mean future fitness gain ($0 \leq t' \leq t$).

The indices can be interpreted as costs of getting guarded too early in females (*FM*), and costs of failure in beginning guarding in males (*MM*). The higher these costs are, the more willing the animals are expected to invest in resistance or guarding attempts. When the indices are positive, there is always something to gain by struggling. Thus, the indices can be interpreted as acceptable levels of struggling cost. The use of the word 'motivation' is justified, since the higher the acceptable cost, the animal should be more intended to struggle.

We exemplify the variation of male and female motivations in time by calculating the motivations for seven different gain functions (cases A–G; Table 2). In cases A and B only one mating is allowed, and the difference between the cases is in the survival values before and during the precopula so that in case A survival before the precopula is slightly better than during the precopula. Case C equals case A, and case D equals case B with the exception that repeated pairing is allowed following the equations (A3–4). Case E otherwise equals case B but repeated mating is allowed following the equations (A10–11). In

TABLE 2

Gain functions used in example cases (A–G) for calculating male or female motivations to fight. For all cases $t = t_p$, $I = 10$, $b = 10$, $c = 1$. $P(t_p)$, m_m , and m_f are given in the equations 3, A4, and A11 respectively

Case	$g(t_p)$	Parameters
A	$S_1^{t-1} S_2^t (b - ct_p)$;	$S_1 = 0.9, S_2 = 0.8$
B	– " –;	$S_1 = 0.5, S_2 = 0.8$
C	$m_p S_1^{t-1} S_2^t (b - ct_p)$;	$S_1 = 0.9, S_2 = 0.8, n = 3$
D	– " –; $S_1 = 0.5$,	$S_2 = 0.8, n = 3$
E	$m_p S_1^t S_2^t (b - ct_p)$;	$S_1 = 0.5, S_2 = 0.8, t_s = 2, n \rightarrow \infty$
F	$P(t_p) S_1^{t-1} S_2^t (b - ct_p)$;	$S_1 = S_2 = 0.9, \lambda = 0.1$
G	$P(t_p) S_1^{t-1} S_2^t (b - ct_p)$;	$S_1 = S_2 = 0.9, \lambda = 0.6$

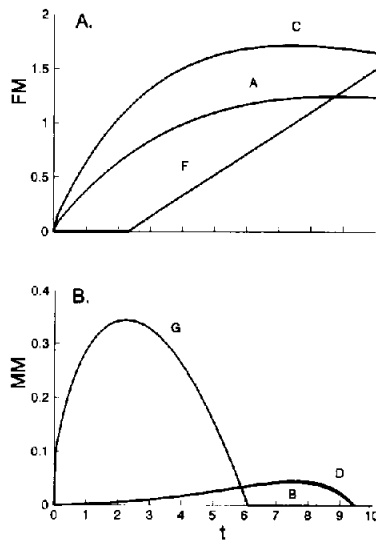


Fig. 5. Relationship between the motivation to fight and the time before parturial ecdysis (t) in females (A) and males (B) calculated according equations (5) and (6) for different fitness gain functions (A–G) defined in Table 2.

cases F and G, the survival rates before and during the precopula do not differ, but the probability of finding a mate is greater in case F than in case G.

Female motivation declines in all cases toward day 0 (Fig. 5A). In case F, in which the female optimum guarding duration is greater than zero, the motivation to resist reaches zero before the parturial ecdysis. In males the motivation curves show a common pattern: in the beginning of the female cycle males show zero motivation. The motivation rises and reaches its maximum, and after that decreases. It is worth noting that the male motivation with gain function E, assuming repeated mating and asynchronous female moulting cycle, gets negative values and reaches zero at $t = 0$.

Conflicts

The conflict, expressed as numerous encounters and intense struggles during these encounters, occurs when both the male and the female are motivated to fight, and ends either in the formation of the precopula or in the separation of the pair after a fight. We define an index (CI) describing the expected strength of this conflict as a product of male and female motivations:

$$CI = FM(i)MM(j) \quad (7)$$

where $FM(i)$ and $MM(j)$ are male and female motivations associated with the fitness gain distributions i and j . Thus defined, the conflict region is restricted to an area where both male and female motivations get positive values. If the gain functions for male and female are equal, then either equation (5) or (6) is negative and thus there is no conflict ($CI = 0$).

However, conflicts may arise if the fitness gain functions differ between the sexes. To exemplify these conflicts, and to analyze the progress of the conflicts in relation to time left

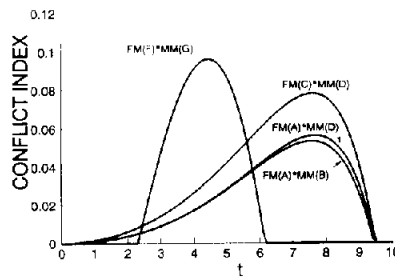


Fig. 6. The conflict index (CI) in relation to time left to parturial ecdysis (t) in six example cases by using the male (MM) and female (FM) motivations calculated from the gain functions (A–G) shown in Table 2.

to female ecdysis, we calculated conflict patterns for certain model cases (Table 2, Fig. 6). At least the following patterns are worth noting:

(1) There is a common pattern of conflicts: at first there is no conflict. After that the conflict arises as males start their guarding attempts, and disappears again as the female motivation to resist decreases.

(2) When the male survival before the precopula is worse than during the precopula and the female survival during the precopula is worse than before the precopula, there is a similar trend in the strength of conflicts towards $t = 0$ independently, whether or not repeated pairing according to the equations (A3–4) is allowed (Fig. 6: $FM(A)MM(B)$, $FM(A)MM(D)$, $FM(C)MM(D)$).

(3) When the probability of finding mates ($P(t)$) decreases with time, and males have a lower $P(t)$ than females, the strength of conflicts decreases faster and reaches zero earlier because female optimum \hat{t}_p is greater than zero (Fig. 6: $FM(F)MM(G)$).

Discussion

Optimal precopula duration

Our analysis of optimal precopula duration revealed two conditions that generated differences between female and male optima. These were: (1) sexual differences in survival rate before and during precopula (Fig. 1); and (2) sexual differences in the probability of finding mates (Figs. 3–4). Both of these conditions are plausible possibilities in *I. baltica*.

Survival differences may arise as a consequence of high mate searching activity of males. During the reproductive period, the swimming activity of males is higher than that of females (Jormalainen and Tuomi, 1989b). The higher activity of males is generally thought to make them more vulnerable to predation (Gwynne, 1989, Magnhagen, 1992), and this is likely to be true in *I. baltica* (unpublished data by Jormalainen, Merilaita and Tuomi). Furthermore, survival during the precopula may be better than during the mate search because of the relatively immobile life style of the pair (Jormalainen and Merilaita, 1993). Female survival, on the other hand, may not differ very much before and during the precopula because of the lower activity of females and the tendency to hide under stones (Salemaa, 1986, Jormalainen and Tuomi, 1989b).

Intrasexual competition is another potential source of conflict in *I. baltica*. The popula-

tion sex ratio of *I. baltica* during the most active breeding season is male biased (Salemaa, 1979), and thus the males' ESS guarding duration should exceed the one of females. Furthermore, the operational sex ratio is even more male biased, further accentuating this difference between sexes. This may be generally true as the operational sex ratio tends to be male biased in species, in which the reproductive investment of females is greater as compared to males (Trivers, 1972; Clutton-Brock and Vincent, 1991). Both Grafen and Ridley (1983) and Yamamura (1987) took into account the sex ratio in their model and predicted, like our model, that the precopula duration of males increases with the proportion of males. What is new in the present analysis is the finding that female ESS differs from the male ESS leading to sexual conflict over start of the precopula.

Consequently, we consider both of these two sources of intersexual conflict as theoretically plausible possibilities. However, the applicability of the sexual differences in survival rates is restricted only to cases where the female moulting cycle is relatively synchronous. Our analysis of male and female ESS guarding durations was also based on synchronous moulting cycles. However, we suppose that operational sex ratios will be male biased in populations with asynchronous moulting cycle, and thus our ESS-analysis should approximate these situations as well. Therefore, we expect that sexual differences in the probability of finding mates may be a more prevalent source of intersexual conflict in mate guarding Crustacea.

Behavioural conflicts

If the male optimum exceeds that of females, a conflict is expected over guarding duration. The actual starting time of the precopula is then eventually determined by the interaction between the male and the female. Our analysis suggests the following pattern of mating behaviour: (1) initially, when females are far from their ecdysis, there is no conflict as males are not motivated to start precopula with immature females; (2) later on, a period of conflict follows when males are motivated to start precopula, while females resist violently; and (3) finally, the conflict disappears close to female ecdysis as females are not motivated to resist precopula attempts any more.

Several behavioural patterns of *I. baltica* are qualitatively consistent with this expected pattern of conflict. Firstly, females stop resisting completely for some time before the ecdysis, and the males detach the female less frequently the closer the parturial ecdysis (Jormalainen and Merilaita, 1993). These patterns fit well to all female motivation curves and to the male motivation curve G, but less well to B and D curves (Fig. 5).

Secondly, the conflict should be most intense (a high number of encounters and intense fights) when males are motivated to start precopula, and females are highly motivated to resist precopulatory attempts. When females are also motivated to start precopula, struggles should be less intense and the number of encounters should decrease in the population due to an increase of more or less permanent precopula pairs. This general pattern is clearly seen in *I. baltica* (Fig. 7) as the number of encounters declines gradually toward the day of ecdysis.

Thirdly, Jormalainen et al. (1994) tested a specific prediction that indirectly arose from the present analysis. When the precopula is established as a result of the behavioural conflict we can, by assuming that the outcome of the struggle is size dependent, predict differences in the precopula duration of different sized individuals. If the size of both the male and the female is important in winning the contest, large males should have longer precopulas than small males, and small females should be taken to precopula earlier than large females by both the large and small males. A laboratory test with *I. baltica* supported

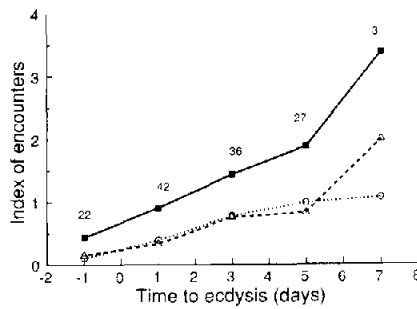


Fig. 7. Index of total number of encounters (mean no. of encounters, during which a struggle occurred, per hour; solid line), and the index in cases where male detached (dashed line) or the female escaped (dotted line) in relation to time left to ecdysis in a laboratory experiment, in which male-female pairs of *Idotea baltica* were reared for two days after which the male was replaced by a new male. Encounters with each male were counted for a certain period of time per day. The data was then arranged according to the time left to ecdysis at the moment of addition of the male in groups of 8-6, 6-4, 4-2, 2-0, and 0-1 days before the parturial ecdysis of the female, and the mean no. of the index for each group was calculated. If the pair formed a precopula during the first encounter it was given a zero index. The mean duration of the precopula in the experiment was 43 h. Numbers in figure refer to numbers of observations for each mean. Total number of females monitored was 42. For details, see Jormalainen and Merilaita, 1993.

this prediction with the qualification that male size has a greater effect on precopula duration than female size.

Finally, a recent manipulative experiment (Jormalainen and Merilaita, submitted) gave strong evidence that female behaviour regulates the start of precopula in *I. baltica*. For control females the average guarding duration was 34 h while a treatment of females by a muscle relaxant increased it to 84 h. Consequently, female resistance undoubtedly is an important aspect in the mating behaviour of *I. baltica*. However, two other mate guarding Crustaceans, *Asellus aquaticus* and *Gammarus zaddachi* (guarding durations: 104 h and 100 h respectively), showed no response to the treatment.

Female choice or intersexual conflict

We have shown above that conditions favouring different precopula durations for males and females exist, and that these conditions can lead to intersexual conflict. Thus, intersexual differences in optimal precopula duration is a plausible hypothesis for explaining the origin of female resistance in mate guarding Crustacea. The demarcation between this hypothesis and active female choice is, however, a difficult task. Plausible expectations of the latter hypothesis could be: (a) that the intensity of female resistance varies depending on the quality of the partner(s), such as male size; and (b) that the female should struggle intensively against low-quality males even close to receptivity if high-quality males are abundant and easily available to her. If the expectation (a) is not true, we consider it unlikely that female resistance represents active female choice. If, on the other hand, the expectation (a) holds, this may not provide conclusive evidence for active female choice because the costs of female resistance may depend on male aggressiveness, which in turn may correlate with male size. The status of the second expectation (b) is somewhat different. If the female always discriminates low-quality males, we consider it to be strong

support of active female choice. If, on the other hand (b) is false but (a) is not, we cannot exclude active female choice, e.g. because female's ability to resist may be constrained by the approaching moult itself. It is also important to note that the hypothesis of differing optimal precopula duration does not, as such, exclude the possibility for female choice. Low-quality males may be less well equipped to overcome the female resistance than high-quality males, and hence female behaviour can cause a systematic bias in male mating success.

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Appendix

Determining conditions for the location of the optimum \hat{t}_p

Let $G(t_p)$ be the lifetime gain function of an individual. $G(t_p)$ is then composed of two functions

$$G(t_p) = m(t_p)g(t_p) \quad (\text{A1})$$

where $m(t_p)$ is the average number of matings of a male that survives to the first mating ($m \geq 1$), and $g(t_p)$ is its success over a single mating episode. Since

$$\frac{dG}{dt_p} = G \left[\frac{d(\ln m)}{dt_p} + \frac{d(\ln g)}{dt_p} \right] \quad (\text{A2})$$

the gain function has two possible optima:

- (1) $\hat{t}_p = 0$ if $dG/dt_p \leq 0$ at $t_p = 0$, and
- (2) $\hat{t}_p > 0$ at which $dG/dt_p = 0$ and $d^2G/dt_p^2 < 0$.

Synchronous moulting cycle

The equation (A1) may take qualitatively different forms depending on the assumptions concerning the female population available. We assume first that the moulting cycle is exactly synchronous in the female population, and that

$$g(t_p) = S_1^{T-t_p} S_2^{t_p} (b - ct_p). \quad (\text{A3})$$

and

$$m_a(t_p) = \frac{1 - S_1^{n(T-t_p)} S_2^{nt_p}}{1 - S_1^{T-t_p} S_2^{t_p}} \quad (\text{A4})$$

Conditions for $\hat{t}_p = 0$

At $t_p = 0$, by using (A3) and (A4), the first derivative of the function (A1) takes the form

$$\frac{dG}{dt_p} = G \left[(1 + x_0) \ln \left(\frac{S_2}{S_1} \right) - \frac{c}{b} \right] \tag{A5}$$

where

$$x_0 = \frac{S_1^T}{1 - S_1^T} - \frac{nS_1^{nT}}{1 - S_1^{nT}}$$

Thus, when $n = 1$ we get for $\hat{t}_p = 0$ the condition

$$S_2 \leq S_1 \exp \left(\frac{c}{b} \right) \tag{A6}$$

and when $n > 1$, the condition

$$S_2 \leq S_1 \exp \left[\frac{c}{b} (1 + x_0) \right] \tag{A7}$$

Conditions for $\hat{t}_p > 0$

If S_2 is higher than allowed by the conditions (A6; $n = 1$) and (A7; $n > 1$) there is $\hat{t}_p > 0$ satisfying $dG/dt_p = 0$ or, from (A2),

$$\frac{d(\ln m_a)}{dt_p} = \frac{-d(\ln g)}{dt_p} \tag{A8}$$

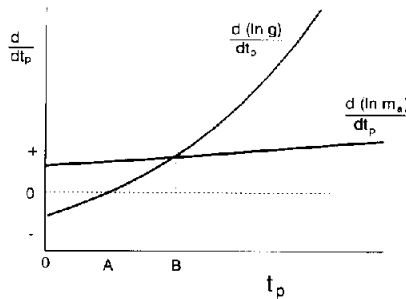


Fig. A1. The location of optimum \hat{t}_p for $dG/dt_p = 0$, or

$$\frac{d(\ln m_a)}{dt_p} = \frac{-d(\ln g)}{dt_p}, \text{ when } n = 1 \text{ (A) or } n > 1 \text{ (B).}$$

When $n = 1$, the left-hand side of the condition (A8) is zero and t_p achieves its optimal value, say A, when the right-hand side equals zero (Fig. A1). When $n > 1$, the left-hand side is positive and an increasing function of t_p , and the optimum value, say B, represents the intersection point of the two curves (Fig. A1). Although $A < B$ (Fig. A1) the changes both in the form of the gain function and the optimal value at t_p are very small above $n = 2$.

For $n = 1$, the optimum precopula duration is

$$\hat{t}_p = \frac{b \ln(S_2/S_1) - c}{c \ln(S_2/S_1)} \quad (\text{A9})$$

Asynchronous moulting cycle

When the female moulting cycle is asynchronous, $\hat{t}_p > 0$ is unlikely to evolve. By assuming a constant duration of mate search, say t_s , that is independent of t_p , the equations (A3) and (A4) can be rewritten

$$g(t_p) = S_1^{t_s} S_2^{t_p} (b - ct_p) \quad (\text{A10})$$

$$m_b(t_p) = \frac{1 - S_1^{n t_s} S_2^{n t_p}}{1 - S_1^{t_s} S_2^{t_p}} \quad (\text{A11})$$

By using (A10) and (A11), the derivative of (A1) at $t_p = 0$ will be

$$\frac{dG}{dt_p} = G \left[(1 + x'_0) \ln S_2 - \frac{c}{b} \right] \quad (\text{A12})$$

where

$$x'_0 = \frac{S_1^{t_s}}{1 - S_1^{t_s}} - \frac{n S_1^{n t_s}}{1 - S_1^{n t_s}}$$

Since $S_2 \leq 1$ and hence $\ln S_2 \leq 0$, the derivative is always negative at $t_p = 0$, and thus $\hat{t}_p = 0$.

Probability of finding a partner

We assume that the probability of finding a partner ($t = t_p$) is

$$P(t_p) = \left(\frac{t_p}{T} \right)^z \quad (\text{A13})$$

and the gain function for $n = 1$ is

$$G(t_p) = \left(\frac{t_p}{T} \right)^z S_1^{T-t_p} S_2^{t_p} (b - ct_p) \quad (\text{A14})$$

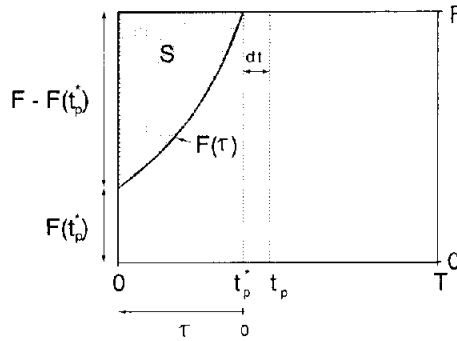


Fig. A2. The decrease in the number of unguarded females (F) after the moment t_p^* when the males start to take females in precopulatory guarding. The guarding criteria of the mutant type is shown by t_p .

Logarithmic derivation yields

$$\frac{dG}{dt_p} = G \left[\frac{z}{t_p} + \ln \left(\frac{S_2}{S_1} \right) - \frac{c}{b - ct_p} \right] \tag{A15}$$

which is always positive at $t_p = 0$ provided that $z > 0$. For $\hat{t}_p > 0$, the expression in the parentheses has to be zero. When $S_2 = S_1$, this condition defines

$$\hat{t}_p = \frac{zb}{(z + 1)c} \tag{A16}$$

indicating that \hat{t}_p increases with positive values of z . Specifically, $\hat{t}_p = 0$ for $z = 0$, and $\hat{t}_p = b/2c$ for $z = 1$ in A16.

ESS conditions for t_p

Let the male guarding criteria be $t \leq t_p$. First, let all males adopt the strategy t_p^* in the population of M males and F females. The number of unguarded females decreases (Fig. A2), starting from the time when males try to guard, according to equation

$$\frac{dF(\tau)}{d\tau} = -aM(\tau)F(\tau) \tag{A17}$$

where $M(\tau)$ is the number of unguarding males and a is a coefficient determining the efficiency of finding a mate. Since the numbers of guarding males and guarded females are equal

$$M(\tau) = M - (F - F(\tau)) \tag{A18}$$

The solution of (A17) and (A18) is

$$F(\tau) = \frac{F(M - F)}{M \exp[(M - F)a\tau] - F} \tag{A19}$$

and, thus, the number of unguarded females at the end of guarding time is $F(t_p^*)$. Therefore, the probability that a male can guard a female until the end is

$$P(t_p^*) = \frac{F - F(t_p^*)}{M} \quad (\text{A20})$$

The average fitness of these males is

$$W(t_p^*) = P(t_p^*)(b - c \text{agt}(t_p^*)) \quad (\text{A21})$$

where $\text{agt}(t_p^*)$ is the average realized guarding time of males that made success in guarding. The value of $\text{agt}(t_p^*)$ is an increasing function of t_p^* but smaller than t_p^* , and can be calculated by

$$\text{agt}(t_p^*) = \frac{\text{area } S}{F - F(t_p^*)} \quad (\text{A22})$$

where area S is shown in Fig. A2.

Suppose now that a mutant male adopting t_p , slightly larger than t_p^* , appears in the population of t_p^* . The probability that the mutant finds a female during the small increment time, $dt = t_p - t_p^*$, is $aFdt$ (Fig. A2). Thus, the fitness of the mutant is

$$W(t_p) = aFdt \left[b - c \left(t_p^* + \frac{dt}{2} \right) \right] + (1 - aFdt)W(t_p^*) \quad (\text{A23})$$

The condition where the mutant cannot invade the population is given by (second order (power) of dt is neglected)

$$dW = W(t_p) - W(t_p^*) = aFdt \left[(b - ct_p^*) - (b - c \text{agt}(t_p^*))P(t_p^*) \right] = 0 \quad (\text{A24})$$

satisfying

$$b - ct_p^* = (b - c \text{agt}(t_p^*))P(t_p^*) \quad (\text{A25})$$

Similarly, we can solve the female ESS. Let us suppose that the female can choose the time to start guarding. The female strategy t_p is that females try to be guarded when the time before ecdysis becomes just t_p . We can use equations (A17)–(A19). The probability that a female can obtain its mate until the end is

$$Q(t_p^*) = P(t_p^*) \frac{M}{F} \quad (\text{A26})$$

and the female ESS satisfies

$$dW = W(t_p) - W(t_p^*) = aMdt \left[(b - ct_p^*) - (b - c \text{agt}(t_p^*))P(t_p^*) \frac{M}{F} \right] = 0 \quad (\text{A27})$$

Note that the first factor is replaced by *aMdt* but this does not affect the result. When $M > F$, comparison between (A24) and (A27) leads to the conclusion that the ESS t_p^* of the female is smaller than that of the males. When $M < F$ on the contrary, the reverse holds. Thus, the more common sex should take the longer optimal guarding time.

References

- Clutton-Brock, T.H. and Vincent, A.C.J., 1991. Sexual selection and the potential reproductive rates of males and females. *Nature*, 351: 58–60.
- Conlan, K.E., 1991. Precopulatory mating behavior and sexual dimorphism in the amphipod Crustacea. *Hydrobiologia*, 223: 255–282.
- Dunham, P.J. and Hurshman, A., 1990. Precopulatory mate guarding in the amphipod, *Gammarus lawrencianus*: effects of social stimulation during the post-copulation interval. *Anim. Behav.*, 39: 976–979.
- Elwood, R.W. and Dick, J.T.A., 1990. The amorous *Gammarus*: the relationship between precopula duration and size-assortative mating in *G. pulex*. *Anim. Behav.*, 39: 828–833.
- Forbes, M.R.L., Pagola, H. and Baker, R.L., 1992. Causes of a non-random pairing by size in the brine shrimp, *Artemia salina* – (Crustacea, Anostraca). *Oecologia*, 91: 214–219.
- Grafen, A. and Ridley, M., 1983. A model of mate guarding. *J. theor. Biol.*, 102: 549–567.
- Gwynne, D.T., 1989. Does copulation increase the risk of predation?. *Trends Ecol. Evol.*, 4: 54–56.
- Hunte, W., Myers, R.A. and Doyle, R.W., 1985. Bayesian mating decisions in an amphipod, *Gammarus lawrencianus* Bousfield. *Anim. Behav.*, 33: 366–372.
- Jormalainen, V. and Tuomi, J., 1989a. Reproductive ecology of the isopod *Idotea baltica* (Pallas) in the northern Baltic. *Ophelia*, 30: 213–223.
- Jormalainen, V. and Tuomi, J., 1989b. Sexual differences in habitat selection and activity of the colour polymorphic isopod *Idotea baltica*. *Anim. Behav.*, 38: 576–585.
- Jormalainen, V., Tuomi, J. and Merilaita, S., 1992. Mate choice for male and female size in aquatic isopod *Idotea baltica*. *Ann. Zool. Fennici*, 29: 161–167.
- Jormalainen, V. and Merilaita, S., 1993. Female resistance and precopulatory guarding in isopod *Idotea baltica* (Pallas). *Behaviour*, 125: 219–231.
- Jormalainen, V. and Merilaita, S., Female resistance and the duration of mate-guarding in three aquatic crustaceans. Submitted.
- Jormalainen, V., Tuomi, J. and Merilaita, S., 1994. Effect of female resistance on size-dependent precopula duration in mate-guarding Crustacea. *Anim. Behav.*, 47: 1471–1474.
- Kroer, N., 1989. Life cycle characteristics and reproductive patterns of *Idotea* spp. (Isopoda) in the Limfjord, Denmark. *Ophelia*, 30: 63–74.
- Magnhagen, C., 1991. Predation risk as a cost of reproduction. *Trends Ecol. Evol.*, 6: 183–186.
- Manning, J.T., 1980. Sex ratio and optimal male time investment strategies in *Asellus aquaticus* (L.) and *A. meridianus* Racovitza. *Behaviour*, 74: 264–273.
- Parker, G.A., 1974. Courtship persistence and female guarding as male time investment strategies. *Behaviour*, 48: 157–184.
- Ridley, M. and Thompson, D., 1979. Size and mating in *Asellus aquaticus* (Crustacea: Isopoda). *Z. Tierpsychol.*, 51: 380–397.
- Salemaa, H., 1979. Ecology of *Idotea* spp. (Isopoda) in the northern Baltic. *Ophelia*, 18: 133–150.
- Salemaa, H., 1986. Ecological and genetic adaptations of *Idotea* spp. (Isopoda, Crustacea). PhD dissertation, University of Helsinki, Helsinki.
- Shuster, S.M., 1981. Sexual selection in the socorro isopod *Thermosphaeroma thermophilum* (Cole) (Crustacea: Peracarida). *Anim. Behav.*, 29: 698–707.
- Strong, D.R., 1973. Amphipod amplexus, the significance of ecotypic variation. *Ecology*, 54: 1383–1388.

- Thompson, D.J. and Moule, S.J., 1983. Substrate selection and assortative mating in *Gammarus pulex* L. *Hydrobiologia*, 99: 3–6.
- Trivers, R.L., 1972. Parental investment and sexual selection. In: B. Campbell (Editor), *Sexual Selection and the Descent of Man*. Aldine Press, Chicago, pp. 136–179.
- Ward, P.I., 1984. The effects of size on the mating decisions of *Gammarus pulex* (Crustacea, Amphipoda). *Z. Tierpsychol.*, 64: 174–184.
- Ward, P.I., 1986. A comparative field study of the breeding behaviour of a stream and a pond population of *Gammarus pulex* (Amphipoda). *Oikos*, 46: 29–36.
- Wickler, W. and Seibt, U., 1981. Monogamy in Crustacea and Man. *Z. Tierpsychol.*, 57: 215–234.
- Yamamura, N., 1987. A model on correlation between precopulatory guarding and short receptivity to copulation. *J. Theor. Biol.*, 127: 171–180.
- Yamamura, N. and Tsuji, N., 1989. Postcopulatory guarding strategy in a finite mating period. *Theor. Popul. Biol.*, 35: 36–50.
- Yodzis, P., 1989. *Introduction to Theoretical Ecology*. Harper and Row, New York, 384 pp.