Priority versus Brute Force: When Should Males Begin Guarding Resources?

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ABSTRACT: When should males begin guarding a resource when both resources and guarders vary in quality? This general problem applies, for example, to migrant birds occupying territories in the spring and to precopula in crustaceans where males grab females before they molt and become receptive. Previous work has produced conflicting predictions. Theory on migrant birds predicts that the strongest competitors should often arrive first, whereas some models of mate guarding have predicted that the strongest competitors wait and then simply usurp a female from a weaker competitor. We build a general model of resource guarding that allows varying the ease with which takeovers occur. The model is phrased in terms of mate-guarding crustaceans, but the same logic can be applied to other forms of resource acquisition where priority plays a role but takeovers might be possible too. The race to secure breeding positions can lead to strong competitors (large males) taking females earliest, even though this means accepting a lower-quality female. Paradoxically, this means that small males, which have fewer breeding opportunities, are more choosy than larger ones. Such solutions are found when takeovers are impossible. The easier the takeovers and the higher the rate of finding guarded resources, the more likely are solutions where guarding durations are short, where strong competitors begin guarding only just before breeding, and where they do this by usurping the resource. The relationship between an individual's competitive ability and its timing of resource acquisition

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can also be nonlinear if takeovers are moderately common; if this is the case, then males of intermediate size guard the longest.

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One of the most common characteristics of mating systems is competition among males—either for females or for resources necessary to achieve matings. A male's success in the competition depends in many cases on when he decides to start the mating period relative to other males. This is clearly important when resources can be reserved by the earliest arrival. Many examples of this arise in territorial systems, including early arrival of migratory birds to occupy the best breeding sites (e.g., Ketterson and Nolan 1983; Cristol 1995; Fransson and Jakobsson 1998; Verboven and Visser 1998; Kokko 1999; Currie et al. 2000), territory defense after the breeding season has ended (Forstmeier 2002), the occupancy of lek territories outside the breeding season (Kokko et al. 1999; Rintamäki et al. 1999), and year-round site tenacity in birds when a migratory strategy would provide better survival (Kokko and Lundberg 2001). The optimal decision here often depends on male ability to defend the territory. Old individuals often arrive earlier than young ones (Ketterson and Nolan 1983), as in reed warblers (Hasselquist 1998) and American redstarts (Francis and Cooke 1986).

Precopulatory mate guarding shares some characteristics with territory guarding, although males guard the females directly instead of the resource of interest to the females. Particularly impressive examples of mate guarding occur in crustaceans with internal fertilization (reviewed by Jormalainen [1998]), where copulation is physically impossible outside a short time window when the female molts. Males, therefore, grab females and carry them in a ventral position for prolonged periods of time before molt (e.g., Ridley and Thompson 1979; Birkhead and Clarkson 1980; Elwood and Dick 1990; Jormalainen and Merilaita 1993). Males attempt to guard only females that have reached some maturity stage, probably because males assess female maturity by the level of molt hormone (Bo-

rowsky 1984, 1985), and males become attracted only if this is higher than their guarding criterion. The problems of male timing and its relation to male quality are clearly related for the cases of migrant arrival and duration of mate guarding; however, a comprehensive theory with which to understand these questions is currently lacking.

Theoretical models predict that when resources vary in quality, high-quality males that suffer lower costs from occupying the resource for a long time should, under relatively general conditions, make their reservations first (Kokko 1999). However, the model of Kokko (1999) assumed that takeovers are not possible. If high-quality individuals are successful in taking over resources from their lower-quality competitors, then theory predicts that the highest-quality competitor should refrain from resource guarding for the longest time and then simply take over the preferred resource item, for example, the most fecund female (Grafen and Ridley 1983).

Thus, the models of Grafen and Ridley (1983) and Kokko (1999) appear to make two opposite predictions. Their assumptions are opposite too; the former assumes that takeovers are always successful and costless, and the latter assumes that they are impossible. In the well-studied amphipod *Gammarus pulex*, takeovers are rare (Ward 1983; Elwood et al. 1987), but takeovers of mates have been empirically demonstrated in at least eight mate-guarding crustacean species (Jormalainen 1998). Among migrant birds, higher-quality individuals, either in terms of fighting ability or ability to bear the costs of earliness, often occupy resources early (Francis and Cooke 1986; Hasselquist 1998). Broom et al. (1997, 2000) model a situation where takeovers are sometimes successful. However, in their models, competitors have equal quality and cannot choose when to make the choice. Their results are therefore difficult to compare with Grafen and Ridley's (1983) and Kokko's (1999).

We provide a general model where both competitors and the resource are allowed to vary in quality, takeovers may or may not be possible, and competitors can vary their choosiness over time in a way that also allows competitors to stay "out of the game" for a period of time. We have formulated our model keeping precopulatory mate guarding in crustaceans in mind because some assumptions we have made (e.g., continuous and asynchronous breeding) are a better approximation of these systems than of, for example, territorial breeding birds. However, we would expect many of our principles to carry over to other systems.

For crustacean mate guarding, theory predicts that a stable guarding criterion should evolve to maximize male mating rate, and this criterion is determined in a game between males (Grafen and Ridley 1983; Yamamura 1987; Yamamura and Jormalainen 1996). The game arises be-cause the optimal criterion for a male must depend on the decision of other males. For example, if all males accept only the best females, a male with a less strict criterion will have a whole female maturity class all to himself (Grafen and Ridley 1983).

Besides costs and benefits for males, a number of other factors have been shown to be important in determining the male criterion. Female resistance can, for example, be very important (Jormalainen 1998). Because being guarded is generally costly for females, they benefit from resisting male guarding attempts (Jormalainen et al. 2000; Sparkes et al. 2000) if this delays the start of guarding. However, the ability of females to resist varies among species and populations (Birkhead and Clarkson 1980; Ward 1984; Elwood et al. 1987; Elwood and Dick 1990; Jormalainen and Merilaita 1995; Jormalainen et al. 2000; Sparkes et al. 2000), and in many cases, females may have small chances of thwarting a male guarding attempt. In our model, females cannot influence guarding duration. There are well-studied cases where this seems to be realistic, and this also makes our model more interpretable in the general case, where resources (e.g., territories) generally do not resist being taken.

To predict how all factors interact in determining the timing of precopulatory mate guarding, we analyze a full dynamic model of a simplified crustacean mating system. We solve numerically for the evolutionarily stable male guarding criterion and make predictions on how possibilities of takeovers and population density affect the outcome.

The Model

We consider the evolution of mate guarding when males meet females that are either single or already guarded by another male. The strategy of a male is reflected by his motivation to begin guarding when encountering a female of a specific maturity, that is, with a certain amount of time left until the next molt. This motivation will be influenced by a number of factors, for example, female availability and the cost of carrying the female. If the female is already guarded, it also depends on the male's own ability to usurp the female from the other male. Let p denote the probability that a male, on meeting a single female, begins to guard her, and let q denote the probability that he attempts a takeover when meeting a paired female. The probabilities p and q are thus a male's strategy. The optimal values of p and q will depend on the male's own size, the female's value (indicated by the time to molt), and, in the case of takeovers, the size of the guarding male. Therefore, before proceeding to the possible forms of these relationships, we first describe the details of the breeding cycle.

The ability to usurp females from other males depends on male resource-holding potential, which is typically correlated with size (Jormalainen 1998). We thus divide the males into different quality classes dependent on their size, m_1, m_2, m_3, etc. Each time a male molts, he grows to a larger size, and the average time between molts is denoted T_C. The maximum male size is m_L, and males of this size do not grow any further when they molt.

Similarly, females remain incapable of mating for, on average, T_C time units after each reproductive molt. A female's quality in this model is simply the proportion (f) of the present reproductive cycle she has completed. Female qualities are divided into K discrete classes and denoted f_1, f_2, f_3, etc., up to f_K. The duration of one maturity class is $T_S = T_C/K$ time units. This equivalence of female quality and maturity means that we assume that no other size or fecundity differences are as important to males as female maturity. This simplification is reasonable when we are interested in modeling the optimal timing of the male guarding criterion. In the mate-guarding isopod *Idotea baltica*, male choice for maturity is much stronger than choice for large size (Jormalainen and Merilaita 1992; Jormalainen et al. 1994). However, this may differ between species (Dick and Elwood 1989, 1990).

To distinguish pairs, we write *mf* to denote pairs, where the male and female qualities are m and f, respectively. This must not be mistaken for a multiplication of the qualities; we use this writing to get a simple notation. The number of single males or females of quality m or f is denoted $n(m)$ or $n(f)$, respectively, and the number of pairs of this type is $n(mf)$. We assume that female resistance has no effect on the male's ability to guard females, and we leave the cases of female control, and mutual control via some antagonistic behavioral interaction (Yamamura and Jormalainen 1996; Härdling et al. 1999, 2001), to future studies.

Unpaired males of quality m acquire unpaired females of quality f at the rate $a(m,f)$, which is calculated as

$$a(m,f) = M_1 n(f) p(m,f). \tag{1}$$

M_1 determines the probability that a single male will encounter a certain single female within one time unit, and this depends on the density of the animals, their mobility, and on how easily they detect each other; $n(f)$ is the number of single females of quality f. The probability that m males and f females form a pair when they meet is $p(m,f)$, which is determined by the motivation of the male to guard the female (i.e., the strategy used by the male).

Bachelors of quality m form pairs via usurpation of another male's female at the rate $\sum_y u(m,yf)$, where $u(m,yf)$ specifies the rate at which bachelor males of quality m usurp females of quality f that are guarded by another male (the victim of usurpation) of quality y. The general expression for $u(m,yf)$ is

$$u(m,yf) = M_2 n(yf) q(m,yf) v(m,y). \tag{2}$$

Note that M_2, the population-specific rate at which singleton males meet pairs, may differ from M_1 because of behavioral differences between singletons and couples. Further, $n(yf)$ is the number of target pairs, and $q(m,yf)$ is the motivation of an m male to usurp an f female from a y male. The function $v(m,y)$ gives the probability that the male succeeds in taking over; this relationship is not influenced by the male's strategy. We assume

$$v(m,y) = \{1 + \exp[\theta(y - m + k)]\}. \tag{3}$$

This is a decreasing function of $y - m$, the quality difference between males. In other words, fights are less often successful against superior competitors. Equation (3) decreases from 1 if $y \ll m$ or to 0 if $y \gg m$. The parameter k specifies the advantage of the male that initially has the female. If $y = m - k$, the winning probability is 0.5. Thus, the larger the value of k, the larger the size difference required for a successful takeover. The rate by which the winning probability increases with size difference is scaled by θ.

The male's strategy is the set of the functions $p(m,f)$ and $q(m,yf)$ that define his "motivation" (i.e., probability) to begin guarding or to attempt a takeover, respectively. In principle, it is possible to search for each value of $p(m,f)$ and $q(m,yf)$ separately. However, this poses computational difficulties because with L male classes and K female classes, there are $KL(1 + L)$ optima to be determined, with every value influencing the optimality of others. To ease the computation and interpretation of results, we have therefore constrained the calculation to specific functional forms of $p(m,f)$ and $q(m,yf)$:

$$p(m,f) = \left(1 - \frac{1}{1 + \exp\{\sigma[f - d_1(m)]\}}\right) \bigg/ \left(\frac{1}{1 + \exp\{\sigma[f - c_1(m)]\}}\right) \tag{4}$$

for the motivation to start guarding a spinster of quality f and

$$q(m,yf) = \left(1 - \frac{1}{1 + \exp[\sigma(y - d_2(m,f))]}\right) \bigg/ \left(\frac{1}{1 + \exp[\sigma(y - c_2(m,f))]}\right) \tag{5}$$

for the motivation to attempt a takeover from a male of quality y that guards a female of quality f. These two func-

tions have the same general, biologically meaningful form; they are flexible enough to allow for strategies that prefer immature females, mature females, or an intermediate maturity class (fig. 1). Note that the different examples of function (4) shown in figure 1 could just as well be a graph of function (5) if we had male quality as the independent variable. For enhanced biological realism, the functions impose a cognitive constraint; males cannot drastically change their perception of females if the female's quality (or, for a guarded female, the guarder's size) changes by a very small degree. The functions use a constraint parameter σ, which determines how sensitive the motivation can be to such changes. In our examples shown, we have used $\sigma = 30$.

When considering functions of the form (3) and (4), a strategy for the male population is described by a set of values of $c_1(m)$, $d_1(m)$, $c_2(m, f)$, $d_2(m, f)$. This reduces the number of values to be calculated from $KL(1 + L)$ to $2[K(L + 1)]$. For example, if we consider seven male qualities and 10 female maturity stages, the strategy consists of 70 values of c_2, 70 values of d_2, seven values of c_1, and seven values of d_1.

Dynamics of the Population

Whether a male should guard a specific female will depend on the availability of other females in the population. This, in turn, will depend on the decisions of other males. To evaluate a male's fitness, we therefore need to derive the dynamics of pair formation and breeding when the population of males uses a resident strategy. Then we can calculate the fitness of a male that deviates from this strategy to see whether any mutant strategies can invade the population.

To describe the dynamics of free and paired males and females of different sizes, we need to specify the death rates of all individuals, the rates of pair formation, and the breakup rates of pairs. We specify how each rate is mathematically derived.

Death Rates

Death rates of single males and females are μ_M and μ_F, respectively. For paired individuals, we assume that the rate of mortality depends on the quality of the paired male, that is, that a function $\mu_P(m)$ determines the rate at which the pair is predated. This construction is made to capture the differential costs of guarding among males of different sizes (Elwood and Dick 1990; Plaistow et al. 2003). We can imagine that variation in male ability to avoid predators is the cause of all variation in pair mortality, for example, if larger males are better swimmers in precopula (Adams and Greenwood 1987). Note that $\mu_P(m)$ deter-
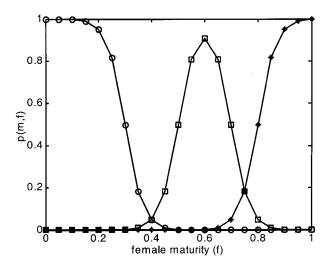

Figure 1: Some possible relations between female maturity (when unguarded) and male guarding motivation. The function $p(m, f)$ may take varying shapes, from increasing to decreasing and humped, dependent on the parameter values c_1 and d_1. The three lines have parameter values according to $c_1 = 0.3$, $d_1 = -1$ (*open circles*); $c_1 = 0.7$, $d_1 = 0.5$ (*open squares*); and $c_1 = 2$, $d_1 = 0.8$ (*asterisks*).

mines the mortality rate for both members of the pair. This is natural because a predator will typically kill both sexes in the attack. Specifically, we use the linear function $\mu_P(m) = a + bm$ with $a = 3.5$ and $b = -1$.

Rate of Pair Formation

A bachelor of quality m forms pairs with females of quality f at the total rate

$$P_F(m, f) = a(m, f) + \sum_y u(m, yf). \quad (6)$$

The first term on the right-hand side is the rate at which the male acquires single females, whereas the second term takes care of pair formation via takeovers.

Breakup Rate of Pairs

The rate at which a male (quality m) that holds a female of quality f loses his female because of takeover by a male of quality y is expressed in equivalence with the earlier expression for gain by takeover:

$$u(y, mf) = M_2 n_1(y)q(y, mf)v(y, m), \quad (7)$$

where $n_1(y)$ is the number of bachelors (see appendix). The total rate at which such a male loses his female is the sum

$$\sum_y u(y, mf). \qquad (8)$$

The dynamics automatically give rise to a probability that a male molts while guarding, and we assume that the pair breaks up if this happens. Although this case has rarely been observed (but see Jormalainen 1998), we choose to keep the model as simple as possible by not including any changes in the male motivation to guard caused by his approaching molt.

Also, because females increase in quality with time, a male that is at present guarding a female with, for example, quality f_1 might soon have a female with the higher-quality f_2 unless she is taken by someone else. The rate at which females increase in quality between stages is $1/T_S$, where T_S is the duration of one quality category. The total rate of pair dissolution for a male in an mf pair, $D(mf)$, is

$$D(mf) = (1/T_S) + \sum_y u(y, mf) + (1/T_C). \qquad (9)$$

The first term on the right-hand side of equation (9) is the rate of female quality increase, and the second sum is the total rate of female loss as a result of takeovers. The third term is the rate at which the male increases in size via growth.

Male Dynamics

Males become sexually mature in the smallest size quality, m_1, at the time-constant rate R, and thereafter they grow to a new size category (m_2, m_3, etc.) each molt. The number of males that are in different states at equilibrium (bachelors or paired) can be described by a dynamic system, which we write out in the appendix. Here, we briefly describe the dynamic state changes, and the dynamic is also depicted by the diagram in figure 2.

Focusing on a male in any given state m_S (fig. 2), the dynamics are governed by the following. The "inflow" of new males is R if m_S is the smallest size, and for larger classes, it is the rate at which males of the smaller size grow (see appendix). If the male is single, three things may happen to him. He may die (rate μ_{IM}), he may start guarding a female of quality f_Q (rate $P_F(m_S, f_Q)$), or he may molt and grow larger ($1/T_C$). If he is already guarding a female, he may lose her to another male ($\sum_y u(y, m_S f_Q)$). The pair may also be predated so that he dies ($\mu_P(m_S)$). Alternatively, he may molt and lose the female in the process ($1/T_C$), or the female may also mature to a higher-quality f_{Q+1} (rate $1/T_S$). If the female is in state f_K and molts, the male fertilizes her eggs and leaves her. The largest male size m_L is a special case because males cannot grow larger, although they are still assumed to molt (see appendix). However, we have chosen parameter values so that the
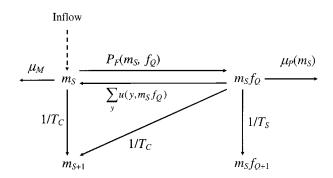

Figure 2: Path diagram showing the different ways in which a male may change state and the rate of these flows. A single male of the quality m_S may suffer mortality (rate μ_{IM}), or he may start guarding a female of quality f_Q (rate $P_F(m_S, f_Q)$). He may also molt and grow larger ($1/T_C$). A guarding m_S male may lose the female because of usurpation by another male ($\sum_y u(y, m_S f_Q)$). The pair may be predated ($\mu_P(m_S)$). If the male molts, he loses the female in the process ($1/T_C$). The female may also mature to a higher-quality f_{Q+1} (rate $2/T_S$). The dotted line directed toward m_S represents the inflow of new single individuals. For the smallest male size, this is the birth rate. For larger sizes, it is the inflow of molting smaller males.

male population is dominated by the smaller size classes and the largest male size class m_L is practically absent. Thus, the upper limit to male size is not expected to influence solutions.

Female Dynamics

For spinsters of quality f, the rate at which they get paired up with males of size m_S is $M_1 n(m_S) p(m_S, f)$ (fig. 3). Once a female is paired, she can become single again only because she herself molts and lays her clutch of eggs or because the partner molts. The number of spinsters can similarly as for males be described by a dynamic system, which is written out in the appendix. Here, we briefly describe how a female may change state, and the reader should consult the diagram in figure 3 for further explanation. Focus on a female of quality f_Q (fig. 3). Three things may happen to a single female of this type. She may die (rate μ_F), she may mature to the higher maturity class f_{Q+1} ($1/T_S$), or she may become guarded by a male of quality m_S. If she is already guarded, the pair may be predated so that she dies ($\mu_P(m_S)$), she may become single via male molt ($1/T_C$), or she may mature to the class f_{Q+1} ($1/T_S$) (fig. 3). Once the female has reached the last maturity stage f_K, she completes her reproductive cycle at the rate $1/T_S$ and enters the lowest maturity class f_1 again. Females enter the lowest maturity class f_1 for the first time at rate R. Thus, we assume equal sex ratio at birth.

Each male strategy is connected with a stable population structure. We use a numeric procedure to compute this
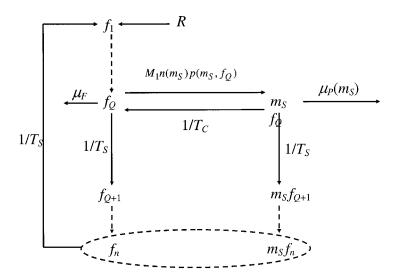
Figure 3: Path diagram depicting the female dynamics. A spinster of quality f_Q may die (at rate μ_F). She may enter class f_{Q+1} ($1/T_S$). She may become guarded by a male of quality $m_S(M_1 n(m_S)p(m_S, f_Q))$. Guarded females may become predated ($\mu_P(m_S)$). Females may also become single via male molt ($1/T_C$) or may mature to the class f_{Q+1} ($1/T_S$; fig. 3). Once the female has reached the last maturity stage f_K, she completes her reproductive cycle at the rate ($1/T_S$) and enters the lowest maturity class f_1 again.

stable population state. First, we assume some distribution of female qualities. This enables us to calculate the stable number of bachelors and pairs by using equations (A1), (A2), and (A3). With these values, we can calculate a new distribution of spinsters using equation (A4). We then go back to equations (A1), (A2), and (A3) and calculate a new stable number of bachelors and pairs. We continue these iterations until a stable distribution is reached.

Mutant Fitness

Now focus on a particular male of, say, the smallest size class m_1. If this male increases his motivation to usurp females of quality f_1 paired with males of quality m_2, this means that this male experiences an increased rate of pair formation $q(m_1, m_2 f_1) + \delta$, compared with $q(m_1, m_2 f_1)$ experienced by the rest of the population. Whether the mutant male strategy will be able to invade the resident population strategy depends on its fitness. Mutant male fitness at time t is the probability $p_{f_K}(t)$ that the mutant male is alive at t and guards a female that is in the last maturity stage f_K, multiplied with the fitness increase rate, which is proportional to the female's rate of completion of the reproductive cycle ($1/T_S$). Lifetime fitness W is the integral of this over time; that is,

$$W = \int_0^\infty p_{f_K}(t)/T_S \, dt = \frac{1}{T_S} \int_0^\infty p_{f_K}(t) \, dt. \tag{10}$$

In the appendix, we show how to compute the fitness of a mutant individual under the assumption of population equilibrium, that is, that population size is stable. The best-reply strategy is the strategy that maximizes mutant fitness given a population strategy J (Motro 1994). The numerical procedure to find the evolutionarily stable strategy (ESS) is as follows. Given the present population strategy J, calculate the stable population structure using equations (A1)–(A4). Then go through all values of c_1, d_1, c_2, and d_2 and pick out the value that maximizes mutant fitness, keeping all other values at their population levels. This is the best-reply strategy I. At each stage s in the iteration to find the ESS, the new population strategy is a mixture of the old values and the best-reply ones, according to the formula

$$J(s + 1) = (1 - \lambda)J(s) + \lambda I(s), \tag{11}$$

where λ is a proportion (Houston and McNamara 1999). Eventually, the population strategy converges to the equilibrium.

This procedure converges to an ESS, but it finds only one ESS at a time. We did not find multiple equilibria of the game, although we note that our numerical procedure is incapable of proving that no multiple stable solutions exist.

Results

The stable strategy consists of a set of rules p and q for when to target females as mates. When plugged into equa-

tions (4) and (5), the evolutionarily stable values of c_1, d_1, c_2, and d_2 specify the probability that a male starts to guard a particular female and the probability of him attempting to take over a female if she is paired already.

Although our functions (4) and (5) allow for a widely varying range of preferences, the stable solutions we found always specified that males prefer relatively mature females; that is, the preference functions were of the shape of the rightmost curve in figure 1. Thus, in all of the following, we describe results by specifying the guarding criterion as the 50% isocline for male motivation. For females whose quality exceeds this criterion, a male is more likely to begin guarding (or to attempt a takeover) than not.

However, the guarding criterion varies across male classes. In figure 4a, the curve separates the regions where a male is likely to attempt to guard a spinster female (right of 50% motivation curve) and where he is not likely attempt to guard (left of 50% motivation curve). In this example, takeovers are impossible ($v = 0$), and a male's mortality increases less when guarding if he is high quality. Apart from the last age class, which is practically nonexistent, the figure shows that the maturity criterion for guarding is less strict for higher-quality males. Counterintuitively, high-quality males accept lower-quality females. Small males, again counterintuitively, have the strictest guarding criterion even though they have few reproductive opportunities. This is because they pay large costs for guarding attempts.

When takeovers are possible but require a large size difference, only the larger male sizes will delay guarding (fig. 4b, *thick line*: when meeting a spinster; *thin line*: when meeting a pair). In this example, males of intermediate size have the least strict guarding criterion. Finally, when takeovers are easy (fig. 4c), the guarding criterion is more strict the higher the quality of the male. This corresponds to the finding of Grafen and Ridley (1983). Therefore, we find a continuum between the findings of Kokko and Grafen and Ridley. The order in which individuals start guarding depends on the size advantage necessary for successful takeover.

The Influence of the Meeting Rate

Increasing the meeting rate (the parameters M_1 and M_2) generally makes the male mate guarding criterion more strict, so males become attracted only to more mature females (fig. 5). If takeovers are possible, increasing the meeting rate M will also change the timing of large and small males relative to each other (fig. 5). With high M, larger males should have a more strict criterion than small males, so the guarding criterion becomes stricter with male size (i.e., the largest males are most choosy). With low M,
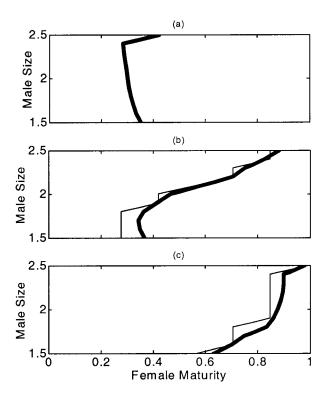

Figure 4: Results from the numerical computations of the evolutionarily stable relation between male size-specific guarding criterion and female maturity. The lines show the evolutionarily stable guarding criterion (50% isocline of male motivation; *thin line*, when meeting a pair; *thick line*, when meeting a spinster). Males begin guarding a female only if she is more mature than this criterion; thus, males with the smallest threshold guard the longest. In *a*, takeover is impossible, and stronger males guard earliest except for the very largest size class, which, in practice, does not exist in the population. In *b*, takeovers require a size advantage, $k = 0.75$. In *c*, the required size advantage is smaller, $k = 0.25$, and largest males guard the shortest time. Other parameters are $M_1 = M_2 = 100$, $\sigma = 30$, $\theta = 10$, $m_1 = 1.5$, $m_L = 2.5$, $L = 11$, $K = 8$, $R = 1$.

the difference between large and small males becomes smaller, so large males have more or less the same criterion as small ones (fig. 5).

It is interesting to contrast the situations $M_1 < M_2$ and $M_2 < M_1$ (fig. 6). In the first case, the probability that a male notices a paired female is higher than if she is single. Both large and small males then have a more strict guarding criterion. Alternatively, if $M_2 < M_1$, pairs are less visible than single individuals (fig. 6). The solution is then similar to when takeovers are impossible, so males of a larger size have a less strict criterion (cf. fig. 4a).

Discussion

Our model shows that for male mate-guarding crustaceans, the evolutionarily stable mate-guarding criterion
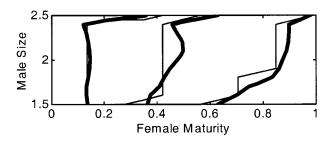
Figure 5: Each pair of lines (*thin line* and *thick line*) show the evolutionarily stable guarding criterion for a given population specific meeting rate. The thin line shows the guarding criterion when meeting a pair, and the thick line shows the guarding criterion when meeting a spinster. Parameter values for the three pair of lines are as follows: left pair of lines, $M_1 = M_2 = 4$; middle pair of lines, $M_1 = M_2 = 10$; right pair of lines, $M_1 = M_2 = 100$. Other parameters are $k = 0.25$, $\sigma = 30$, $\theta = 10$, $m_1 = 1.5$, $m_L = 2.5$, $L = 11$, $K = 8$, $R = 1$.

depends on male size and that large males may have either lower or higher thresholds for female maturity (i.e., start guarding earlier or later), compared with smaller males. The relation between male size and guarding criterion may also be complex, with intermediate-size males having the least strict threshold. This variation is caused by two factors with similar effects: the size advantage necessary for successful takeover (k) and the mixing rate or "viscosity" of the population, as reflected by the meeting rate parameters M_1 and M_2. If takeovers are impossible, males will compete over mates by the choice of precopula duration. If large males can better bear the costs of guarding, for example, if they are better swimmers when guarding (Adams and Greenwood 1983), they can afford to guard for longer; that is, they guard less mature females. This leads to large males having longer precopulatory guarding than smaller males, as found in *Gammarus* (Elwood and Dick 1990; Hume et al. 2002). Because the game between males is similar to an arms race in accepted guarding duration, the average duration of mate guarding is predicted to be long, compared with when takeovers are possible.

A similar result was found by Kokko (1999) in a model of migrant bird arrival where territory takeovers were impossible. She predicted that large males should arrive first to the breeding grounds because they are better able to withstand the adverse weather conditions early in the breeding season and that the race for breeding positions causes males to pay significant costs for arriving much earlier than would be optimal. In Kokko's (1999) model, the outcome is quite intuitive because early males obtain the best resources. In our mate-guarding example, however, the same result appears to be somewhat counterintuitive; best males, by accepting to guard earlier, also au-

tomatically obtain lower-quality females (i.e., those who have longer to molt). That it nevertheless pays to accept such females suggests that the race to secure breeding possibilities is a strong selective agent in a diverse range of breeding systems. Large males, despite their longer guarding duration, fertilize eggs at a higher rate because their preemptive guarding means that small males often end up with no females at all during a breeding cycle. Small males do not benefit from guarding early, not because their guarding attempts would fail because of takeovers (which are impossible under this scenario) but because they suffer from too high mortality costs when guarding.

If large males may take over females from smaller males, competition between males is no longer tied to the duration of precopula. Large males do not have to choose females with a very long time until molt but can rely on their ability to take over already guarded females instead. As a result, the arms race between males in precopula duration collapses, and the average duration of precopula becomes much shorter for all male sizes (fig. 4*c*). Larger males choose to guard later than smaller males and have shorter precopulatory guarding. This result confirms the result of Grafen and Ridley (1983).

These two cases are connected by a continuum of cases where takeovers require an increasing size advantage. When only the largest males are able to take over females from the smallest males, the male population is, in practice, divided into three classes. The largest and the smallest males are involved in an evolutionary game with each other. Large males delay guarding because they rely on their ability to usurp females from the smallest males. Males of intermediate size are relatively safe from the risk of usurpation but also have small chances of taking over females from other males. They are therefore caught in the arms race of precopula duration and evolve a less strict
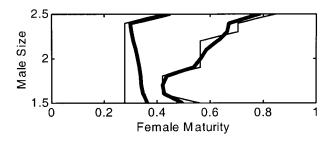

Figure 6: Effect of unequal population-specific meeting rates M_1 and M_2. The thin lines shows the guarding criterion when meeting a pair, and the thick line shows the guarding criterion when meeting a spinster. For the left two lines, $k = 0.25$, $M_1 = 100$, $M_2 = 1$. For the right two lines, $k = 0.25$, $M_1 = 1$, $M_2 = 100$. Other parameters are $\sigma = 30$, $\theta = 10$, $m_1 = 1.5$, $m_L = 2.5$, $L = 11$, $K = 8$, $R = 1$.

maturity criterion than other size classes. This is seen in figure 4*b*. The thick line shows the criterion for guarding single females. The intermediate male size class is least choosy and begins guarding females earlier.

The solutions depend on how often males find resources, as indicated by the parameters M_1 and M_2. Their effect depends on the size advantage required for takeovers. If takeovers are impossible, the rate of meeting paired individuals (M_2) has no influence at all on the solutions, as expected. Increasing the rate at which single males encounter single females (M_1), then, leads to all males being more choosy. For example, in populations of *Gammarus* with a female-biased sex ratio, and hence single males being more likely to encounter single females, the guarding durations were shorter than without the sex ratio bias (Dick and Elwood 1996). Largest males have the longest precopula in this case. If takeovers are possible, variation in the meeting rate may also change the shape of the relation between male size and guarding criterion. Consider the case where there are no behavioral differences between pairs and single individuals so that $M_1 = M_2 = M$ (fig. 5). With low M, the pattern is similar to the case when takeovers are impossible, in that the difference in the guarding criterion between large and small males becomes smaller (fig. 5). When the meeting rate increases, it is mainly the larger males that delay the onset of guarding.

The two cases $M_1 < M_2$ and $M_2 < M_1$ contrast two situations. If pairs are less easy to find than single individuals, we have $M_2 < M_1$; pairs may, for example, be hiding from predators. In this case, the solutions become similar to when takeovers are assumed impossible (cf. fig. 4*a*). This is intuitive; when males very infrequently meet pairs, they choose their criterion as if the females in pairs were more or less inaccessible, regardless of how easy takeovers would be when encountering a pair. Ward and Porter (1993), for example, suggested that paired *Gammarus* hid in crevices in the substrate and that this protected the paired male against takeovers. By contrast, if $M_1 < M_2$, pairs are much more easily detected than single females ($M_1 < M_2$) either because they are more immobile or simply because the pair is a larger object than a single female (fig. 6). In many mate-guarding crustaceans, the female is smaller than the male (e.g., Jormalainen et al. 2000), so guarded females may be easier to find. In this case, takeovers may become an important way to acquire a female, so the tendency increases for large males to have a stricter criterion (fig. 6).

Size-assortative mating, with large males guarding large females, is often found in mate-guarding crustaceans (Crespi 1989). Our model does not include variation in female size, but large females typically produce more eggs and are thus more valuable (Birkhead and Clarkson 1980).

When takeovers are rare, the best option for mate-searching males must be to choose the best single female available, and that is likely to be a large female (Elwood et al. 1987). Because large males take females further from the molt, the largest and most fecund females will become paired with large males. This leaves the smaller and less fecund females to the smaller male size classes, and these smaller females will be guarded for a shorter time. Elwood and Dick (1990) found that both male and female size were positively correlated with precopula duration. The result will be a positive correlation between male and female size in pairs, brought about by the timing of the start of precopula (Elwood and Dick 1990; Hume et al. 2002). If takeovers are possible, however, the situation becomes more complicated. Whether a male will attempt to guard a female of a given quality/size may then depend on the probability that he will be able to guard the female until her molt. If he risks injury and losing the female in a takeover, he might not attempt to guard a highly fecund female. Also, whether a male will attempt a takeover depends on whether female size can be assessed when the female is already guarded. It would be possible to alter the model to take female size/fecundity into account, but the evolution of size-assortative mating is not our main interest here.

Many details of our model, for example, that the resource has a molt schedule and a death rate, have been assumed keeping crustaceans in mind, but the problems of choosiness, timing, and takeovers apply generally to essential breeding resources that are taken preemptively (Broom et al. 1997, 2000; Kokko 1999). Some of the key conclusions from our model can be applied to the general case. Let us take territorial acquisition as an example. In territory acquisition, there may be consistent differences in territory values that do not change over time, in contrast to when early guarding automatically means that a female's quality is low. If territory takeovers were quite easy and predictable according to body size, one would expect high-quality individuals to arrive late and then simply usurp another owner from a suitable territory. The reason why the initial territory owners should bother in the first place is that they might get away unnoticed. A "cascading" race to arrive early (Kokko 1999) would then not be observed. Such a strategy has indeed been described for territorial male sticklebacks *Gasterosteus aculeatus*; large males were found to arrive later than small males because they were able to take over territories on arrival (Candolin and Voigt 2003).

If territory takeovers are less easy but still possible, we may find solutions where intermediate males arrive earliest. This is a further example of the fact that the relationship between an individual's quality and its behavior is often nonlinear in timing games. Such solutions have

been found for arrival times in a territorial game (Kokko 1999) and for guarding duration of female salmonids who protect their eggs before dying (Morbey and Ydenberg 2003; this article also features an analytical explanation for why the most extreme behavior can be found in intermediate individuals).

APPENDIX

Male and Female Dynamics

We present the dynamic systems for the number of single and paired individuals of different male size classes (fig. 2). Males are born into the smallest size class at the rate of R per time unit. We assume that females may have K different qualities $f_1, f_2, f_3, f_4, \ldots, f_K$, where f_K is the quality that is nearest to molting. The dynamics for m_1 are given by

$$((-1/T_C) - \mu_M - \sum_f P_F(m_1, f))n(m_1) + \sum_{i=1}^{K} \sum_y u(y, m_1 f_i)n(m_1 f_i) = -R,$$

$$P_F(m_1, f_1)n(m_1) - [\mu_P(m_1) + D(m_1 f_1)]n(m_1 f_1) = 0,$$

$$P_F(m_1, f_2)n(m_1) + (1/T_S)n(m_1 f_1) - [\mu_P(m_1) + D(m_1 f_2)]n(m_1 f_2) = 0, \ldots, \tag{A1}$$

$$P_F(m_1, f_K)n(m_1) + (1/T_S)n(m_1 f_{K-1}) - [\mu_P(m_1) + D(m_1 f_K)]n(m_1 f_K) = 0.$$

If a guarding male molts, he is assumed to lose the female he is guarding. This means that for larger male sizes than m_1, we must consider the increase in number of bachelors resulting from the molt of smaller males. For the male size m_S, $S > 1$; the increase in the number of bachelors is not the birth rate R, as in equation (A1), but instead

$$(1/T_C)\left[n(m_{S-1}) + \sum_f n(m_{S-1}f)\right]. \tag{A2}$$

For the largest male size m_L, the dynamics are different again because males do not grow any larger. That is, single individuals are not "lost" from the size class because of growth. The first equation in the dynamic system for this size is (cf. eq. [A1])

$$\left(-\mu_M - \sum_f P_F(m_L, f)\right)n(m_L) + \sum_{i=1}^{K} \sum_y u(y, m_1 f_i)n(m_1 f_i)$$

$$= (-1/T_C)\left[n(m_{L-1}) + \sum_f n(m_{L-1}f)\right]. \tag{A3}$$

The female reproductive cycle is completed by the reproductive molt. After the reproductive molt, the female is again in the lowest maturity class f_1. The female dynamics are explained in the text and figure 3. The dynamic system for the distribution of unpaired females of all maturity classes is

$$\left(-\mu_F - (1/T_S) - \sum_m M_1 n(m)p(m, f_1)\right)n(f_1) + n(f_K)/T_S + \sum_m n(mf_1)/T_C + \sum_m n(mf_K)/T_S = -R,$$

$$n(f_1)/T_S + \left(-\mu_F - (1/T_S) - \sum_m M_1 n(m)p(m, f_2)\right)n(f_2) + \sum_m n(mf_2)/T_C = 0, \dots, \quad \text{(A4)}$$

$$n(f_{K-1})/T_S + \left(-\mu_F - (1/T_S) - \sum_m M_1 n(m)p(m, f_K)\right)n(f_K) + \sum_m n(mf_K)/T_C = 0.$$

The term $-R$ applies for females as well as for males because the total number of females at birth equals the total number of males (i.e., the sum over all male qualities) at birth, assuming a $1:1$ primary sex ratio.

Mutant Fitness

Now we fasten attention on a mutant male of the smallest size class m_1. The mutant has a different strategy than do the other individuals in the population. This difference is reflected in the rate of pair formation P_F, where the mutant uses P_F^* instead of the population average. The difference might alter his motivation to usurp females from others, or there might be other differences in guarding criterion. If an individual male changes his strategy in this way, this will affect his probability of pairing with a female and also the probability distribution over the female qualities in pairs he may form. To find out whether the mutant male strategy will be able to invade the resident population strategy, we need to know the probability $p_S(t)$ that the male using the strategy is alive and single at time t and for all female qualities $f_1, f_2, f_3, \dots$, the probability $p_{f_i}(t)$ that he is alive and in a pair with a female of that quality at t. In other words, we want to solve the initial value problem

$$\frac{dp_s}{dt} = \left((-1/T_C) - \mu_M - \sum_f P_F^*(m_1, f)\right)p_S(t) + \sum_y u(y, m_1 f_1)pf_1(t) + \dots \sum_y u(y, m_1 f_2)p_{f_2}(t) = 0,$$

$$\frac{dp_{f1}}{dt} = P_F^*(m_1, f_1)p_S(t) - [\mu_P(m_1) + D(m_1 f_1)]p_{f_1}(t) = 0,$$

$$\frac{dp_{f2}}{dt} = P_F^*(m_1, f_2)p_S(t) + (1/T_S)p_{f_1}(t) - [\mu_P(m_1) + D(m_1 f_2)]p_{f_2}(t) = 0, \quad \text{(A5)}$$

$$\frac{dp_{fK}}{dt} = P_F^*(m_1, f_K)p_S(t) + (1/T_S)p_{f_{K-1}}(t) - [\mu_P(m_1) + D(m_1 f_K)]p_{f_K}(t) = 0, \dots,$$

$$\{p_S(0) = 1, p_{f_1}(0) = 0, p_{f_2}(0) = 0, \dots, p_{f_K}(0) = 0\}.$$

The initial condition arises from the fact that a male is single when entering the population; thus, $p_S(0) = 1$. Mutant male fitness at time t is the probability that the mutant male is alive and has a female that is in the last maturity stage, that is, $p_{f_K}(t)$, multiplied by the fitness increase rate, which is proportional to her rate of completion of the reproductive cycle ($1/T_S$). Lifetime fitness W is the integral of this over time; that is,

$$W = \int_0^\infty p_{f_K}(t)/T_S \, dt = \frac{1}{T_S} \int_0^\infty p_{f_K}(t) \, dt. \quad \text{(A6)}$$

The equation system (A5) holds only if the mutant is in the smallest size class. For other classes, we must use other systems, corresponding to dynamics of the type in equations (A2) and (A3).

   If the population size is stable, the number of males found in different states is proportional to the amount of time

an individual male spends in the different states. This means that we can solve for the average amount of time the mutant male spends in all states by solving the system

$$\left(-\mu_M - \sum_f P_F^*(m_1, f)\right)\Delta p_S(m_1) + \sum_y u(y, m_1 f_1)\Delta p_{f_1}(m_1) + \sum_y u(y, m_1 f_2)\Delta p_{f_2}(m_1) + \sum_y u(y, m_1 f_K)\Delta p_{f_K}(m_1 f_K) = -1,$$

$$P_F^*(m_1, f_1)\Delta p_S(m_1) - [\mu_M(m_1) + D(m_1 f_1)]\Delta p_{f_1}(m_1) = 0,$$

$$P_F^*(m_1, f_2)\Delta p_S(m_1) + \Delta p_{f_1}(m_1)/T_S - [\mu_M(m_1) + D(m_1 f_2)]\Delta p_{f_2}(m_1) = 0, \ldots,$$

$$P_F^*(m_1, f_K)\Delta p_S(m_1) + \Delta p_{f_K}(m_1)/T_S - [\mu_M(m_1) + D(m_1 f_K)]\Delta p_{f_K}(m_1) = 0,$$

$$(A7)$$

where $\Delta p(m) = \int_0^\infty p(t)dt$, with $p(t)$ calculated for a particular male quality m. This solution enables us to calculate the fitness of the mutant (A6).

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