

The evolution of prudent choice

Roger Härdling^{1*} and Hanna Kokko^{2,3}

¹Department of Animal Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden,
²Laboratory of Ecological and Evolutionary Dynamics, Department of Ecology and Systematics,
University of Helsinki, Helsinki, FIN-00014, Finland and ³School of Botany and Zoology,
Australian National University, Canberra, ACT 0200, Australia

ABSTRACT

Question: What mate choice strategies are evolutionarily stable when individuals vary in quality and there is competition over mates?

Mathematical method: We analyse a life-history-based game theoretical model of a mating system. The evolutionarily stable strategy (ESS) may be random mating, or any kind of assortative mating dependent on the numerical values of a set of probabilities. We solve for the evolutionarily stable probability values.

Key assumptions: Males of high or poor competitive ability pair with highly or poorly fecund females, and can also attempt to take over a female if she has already paired. Only one sex plays an active role in mate choice.

Conclusions: We show that increased opportunities for a successful takeover favours the evolution of 'prudent' mate choice, where low-quality males reject high-quality females, and high-quality males reject low-quality females. This solution may also evolve because of high fighting costs. Alternative parameter settings lead to solutions where only one class of males discriminates between females, or when all males mate indiscriminately. We calculate the correlation between male and female quality in pairs, and show that this correlation may be positive, zero or even negative, depending on the ESS mate choice strategy.

Keywords: assortative mating, evolutionarily stable strategy, game theory, life-history model, mate choice, mate competition, non-random mating, takeover.

INTRODUCTION

Assortative mating, where traits such as attractiveness, body size or age covary between members of pairs, is a taxonomically widespread phenomenon (Crespi, 1989; Kirkpatrick *et al.*, 1990). Examples range from size-assortative mating in *Drosophila malerkotliana* (Hegde and Krishna, 1997) to high correlations in attractiveness ratings between members of human couples (Kalick and Hamilton, 1986). Examples of traits that have been found to correlate within members of pairs are age (Black and Owen, 1995), reproductive quality (Rintamäki *et al.*, 1998), ornamental traits (Andersson *et al.*, 1998) and sense of humour (Priest and Thein, 2003). Assortative mating can arise as a side-effect of population dynamics (e.g. Ferrer and Penteriani, 2003), but it is often thought to

* Author to whom all correspondence should be addressed. e-mail: roger.hardling@zoekol.lu.se
Consult the copyright statement on the inside front cover for non-commercial copying policies.

reflect a mate choice pattern where members of one or both sexes are more choosy if they perceive themselves to be of high quality (Parker, 1983; McNamara and Collins, 1990; Johnstone *et al.*, 1996; Johnstone, 1997; Itzkowitz and Haley, 1999; Amundsen and Forsgren, 2003; Buston and Emlen, 2003). There is evidence that assortative mating can result from such an active process; for example, size assortative mating in garter snakes (*Thamnopsis sirtalis parietalis*) is caused by size-dependent courting strategies in males (Shine *et al.*, 2001, 2004). Large males court only large females, which are more fecund, while small males court both large and small females (Shine *et al.*, 2001, 2003). In a study on humans (Buston and Emlen, 2003), the greatest amount of variation in the selectivity of mate preference in categories such as wealth and physical appearance was found to be explained by self-perception in the same category of attributes, which also suggests an active behavioural basis for assortative mating.

Demonstration of variation in mate preferences (see Jennions and Petrie, 1997) gives rise to a natural question: Exactly why do different individuals make different choices? The differences might be adaptive if different individuals maximize their fitness by mating with different partners, but to evaluate this hypothesis one needs to understand how different preferences would affect the reproductive success of a given individual. One important factor for the optimal choice of partner is intra-sexual selection (Shine *et al.*, 2001). For example, size-specific courting in garter snakes has evolved because large males are able to exclude mating by their smaller rivals, which are unable to win copulation fights with large males (Shine *et al.*, 2000). For the small males, therefore, courting small females is more likely to be ultimately successful than courting large females (Shine *et al.*, 2001).

Assortative mating can clearly emerge when individuals differ in their preferences (Crespi, 1989), for example if weaker competitors or less attractive individuals are less choosy (Bergstrom and Real, 2000; Fawcett and Johnstone, 2003). However, we lack a general theoretical framework for predicting the evolution of different mate preferences and assortative mating from environmental factors and biological factors such as mate competition. Our aim here is to provide such a theoretical framework. We develop a game-theoretical model of a mating system, where we explicitly consider the costs of mate competition in their life-history context, and the dynamical changes in population size they may cause. For example, any mortality risk associated with competition for mates will influence the population structure, and this will in turn be reflected by the evolutionarily stable mate preference strategy. These ties are frequently important when considering the evolutionary stability of mating systems (Houston and McNamara, 1999, 2002; Webb *et al.*, 1999). For simplicity, we consider a setting where one of the sexes is passive and thus can be ‘owned’. This excludes the computational complications that arise when both sexes perform mate choice. The choosing sex is therefore the same sex that competes over matings. Although this is a relatively little studied scenario (Kokko and Monaghan, 2001; Fawcett and Johnstone, 2003; Härdling *et al.*, 2004), there is increasing recognition that male mate choice plays a role in shaping mating systems (Riechert and Singer, 1995; Amundsen and Forsgren, 2001, 2003; Bonduriansky, 2001; Saether *et al.*, 2001). Also, in mutual mate choice systems, the male choice strategies we focus on in our analysis should theoretically influence the mating structure of the population much more strongly than female choice of suitors (Bergstrom and Real, 2000). We also now have evidence that competitive strategies often are more subtly fine-tuned than previously realized (Craig, 2002; Reinhold *et al.*, 2002; Wedell *et al.*, 2002; Preston *et al.*, 2003; Shine *et al.*, 2004).

We find a large number of evolutionarily stable state-dependent mate choice strategies, and map these onto a parameter space where different biological and environmental factors are varied. We find conditions where some individuals show what we call ‘prudent choice’ – that is, they actively avoid partners that are ‘too good for them’. By this we mean a situation

where an individual prefers a potential mate B over mate A, even though pairing with A, if successful, would yield higher fitness. Such a situation can evolve when the probability of success is lower when attempting to pair with A than with B. One would typically expect that competition for possession of higher quality items is stronger than for lower quality items (Sutherland, 1996). If competition makes it costly to go for the best available option, then individuals of weaker competitive ability might benefit from ignoring too high quality options (Parker and Sutherland, 1986; Alatalo *et al.*, 1992; Sutherland and Parker, 1992).

A similar result was found by Fawcett and Johnstone (2003) in a model of male mate-choice before the start of the breeding season. In this model, both high- and low-quality males preferred high-quality females most of the time. The authors showed, however, that if competition among males is sufficiently costly, and if it is easy for high-quality males to take over females from low-quality males, then low-quality males lower their preference for high-quality females, and may even come to prefer low-quality females. However, their model is based on assumptions such as a fixed time horizon and fixed population size, which restrict the range of cases to which their model applies. In contrast, we report results that apply in a general life-history framework that takes into account the whole lifetime of an individual. By exploring the biological parameter regions where different solutions to the game are found, we find a much larger range of solutions than Fawcett and Johnstone (2003). For example, there are conditions under which more competitive males become less discriminating than poor quality males. We show that this may lead to negative assortative mating. Our model also automatically takes into account the numerical dynamics at the population level, and is thus self-consistent (Houston and McNamara, 1999).

Our model is designed to be able to examine a variety of different conditions, and we describe the evolutionarily stable strategies that arise through the feedback between individual behaviour and population structure. We emphasize the way that these evolutionarily stable mating strategies affect assortative mating of individuals with respect to their quality. We show that female mating rate may be negatively correlated with female quality, for example if high-quality females only are courted by a fraction of the males while all males court low-quality females. Our modelling also applies to cases where the resource to be chosen is not a female, but another defendable resource that can vary in quality, such as a feeding territory or a nest site.

THE MODEL

We assume that males choose among resources necessary for breeding, and that both resources and males vary in quality. This general situation frequently arises in many mating systems: males choose between good and poor resource patches, or they choose between females of varying perceived quality. We model choosiness as variation in the 'motivation' of an individual to attempt to obtain a certain resource item, while noting that motivation does not necessarily lead to ownership (if there is competition over the resource, or if the individual simply fails to locate the desired item). The relationship between resource quality and an individual's motivation to gain it will depend on a number of factors: the quality of the resource, the availability of other resources of higher quality, the choosing individual's own quality, and the costs associated with maintaining ownership of the resource. Although our model assumes male choice, we note that the main results might be applicable to mutual mate choice, because with mutual choice the strongest influence on mating structure may lie in the hands of the males that choose with whom they attempt to mate (Bergstrom and Real, 2000).

Our model of optimal choice is used to determine whether a preference for the highest quality resources maximizes fitness, or if choice is expected to become prudent under some conditions. Our model is built along the same principles as that of Härdling *et al.* (2004): choosers (males) encounter resources (females) at a predefined rate one at a time, and have to decide whether to attempt to own the resource item or carry on searching for new ones. While female ‘quality’ in Härdling *et al.* (2004) is only tied to reproductive maturity associated with female moult, we now assume that females are born with individual differences in fecundity that are constant over time, which makes the model applicable to a wider range of taxa. Also, in contrast to Härdling *et al.* (2004), we include an explicit risk of mortality associated with fights.

Let $q_{y'x}$ denote the probability that a male of quality y' , upon encountering a female of quality x , decides to acquire (i.e. pair up with) her, and let $q_{y'yx}$ denote the probability that he attempts to take over the female of quality x when she is already guarded by a male of quality y . Note that the notation $y'x$ refers to pair formation rather than multiplication. An individual’s strategy is defined by the values of q that it uses. We assume that the male has to spend a certain amount of time, T , in mating and/or paternal activities, such as mate guarding or feeding the offspring, if he mates with the female. Thus, on average it takes time T before the male can receive any benefit from the mating, and during this time he cannot access other females. We assume that T is exponentially distributed. After breeding is completed, the male leaves the female to search for other females. The evolutionarily stable values of q will depend on the choosing individual’s own quality (which determines its fighting ability, e.g. through body size), the females’ quality and, in the case of takeovers, the size of the guarding individual.

Resource-holding potential is assumed to determine the ability to usurp resources from others. We assume that resource-holding potential is correlated with male quality, which we can equate with size without loss of generality. Choosing males are thus classified into large males and small males. Let n_L be the number of large males and n_s the number of small males. Females are divided into a highly fecund (average productivity P) and a poorly reproducing (average p) class. We use notation such as n_{LP} to denote the number of pairs where the male is large and the female is highly fecund.

Large males acquire productive single females at the rate a_{LP} , which is calculated as:

$$a_{LP} = M_1 n_p q_{LP} \quad (1)$$

The parameter M_1 denotes the meeting rate of males and females. It equals the probability that a single male will find a certain female within one time-unit, and depends on the mobility of the individuals, and on how easily males detect females. The variable n_p is the number of unguarded highly productive females. The probability that the large male chooses the highly productive female upon finding her is q_{LP} . In other words, q_{LP} is the motivation of the L male to guard P females. In total, there are four such probabilities, q_{LP} , q_{LP} , q_{sP} and q_{sp} . We do not include any direct interference male competition for mates, which could otherwise decrease the mating rate when the operational sex ratio is very high.

Large males without a female usurp productive females from small males at the rate u_{LsP} :

$$u_{LsP} = M_2 n_{sP} q_{LsP} v_{Ls} \quad (2)$$

Note that M_2 , the population-specific rate at which an individual male finds guarded females, may differ from M_1 . However, in all our calculations and in the examples presented

below, we let $M_1 = M_2$. n_{sP} is the number of small male-productive female pairs. q_{LSP} is the probability that a large individual (L) tries to usurp a productive female (P) from a small male (s) upon an encounter. For each male size, the probability that the male makes a takeover attempt is defined by four such values of q , one for each type of pair he may encounter. In total, there are thus 12 values of q (q_{LP} , q_{Lp} , q_{sP} , q_{sp} and q_{LLP} , q_{LsP} , \dots , q_{ssp}). The variable v_{Ls} is the probability that a large male succeeds in taking over a female from a small male. With two male size classes, we need four such probability values, v_{LL} , v_{Ls} , v_{sL} and v_{ss} , to account for all combinations.

The male strategy is defined by the values of q , which range between 0 and 1. The values of v , on the other hand, are fight outcomes that cannot be chosen by the male, but result from an interaction between males and their sizes. The game can be solved for any values of v , but for simplicity we concentrate on cases where only large males can take over females, and only from small males. Thus all v 's are assumed to be zero except v_{Ls} , which can take any value between 0 and 1.

We will examine the effect of costly usurpation, which arises because the loser in the fight between the guarding male and the attacking male has a small probability of dying because of injury. We assume that the probability that the loser survives is S , and that all winners survive. This will have an effect on the dynamics of the male population (see Appendix and below).

Dynamics of the population

The decision whether to choose a certain female depends on the availability of other females, which is a function of the choices of all the other individuals. This means that we need to model the dynamics of the choosing process to determine the stable number of individuals and the correlation between male and female quality – that is, the assortative mating. Only with this information is it possible to go further with the calculation of the evolutionarily stable strategy (ESS) and find out the most rewarding behaviour of mutant males. This procedure also makes the model self-consistent (Houston and McNamara, 2002).

Death rates

We assume that the bulk of mortality occurs in the single state: the mortality rate is μ for single individuals, and μ' for paired individuals. We assume that mortality always occurs for both members of a pair simultaneously (e.g. through predation).

Rate of pair formation

A male of quality L forms pairs with highly productive females at the rate

$$F_{LP} = a_{LP} + \sum_y u_{LyP} \quad (3)$$

The first term on the right-hand side is the rate of pairing with single females (equation 1), and the second is the rate of takeover of females (equation 2), summed over all guarder sizes. Throughout, analogous expressions are derived for other combinations for individuals, for example small males pairing with poorly productive females. These equations are obtained by simply changing subscripts, and for brevity we have omitted them here.

Break-up rate of pairs

The rate at which a male (quality L) that has a female of quality P loses her because of a takeover by an individual of quality y is, expressed in equivalence with the earlier expression for gain by takeover:

$$u_{yLP} = M_2 n_y q_{yLP} v_{yL} \quad (4)$$

where n_y is the number of males of quality y without a female (see Appendix). The overall rate at which the large male loses the female because of takeovers is

$$\sum_y u_{yLP} \quad (5)$$

The overall rate of pair termination for a large male with a productive female is

$$D_{LP} = 1/T + \sum_y u_{yLP} + \mu' \quad (6)$$

The first term on the right-hand side of (6) is the rate by which the individual leaves the resource after having completed mating. We assume that individuals cannot choose to stay guarding the female after this. The second term is the total rate of female loss due to takeovers, and the third term relates to death of both members of the pair.

Male and female dynamics

Large and small males are recruited into the population at the rates B_L and B_s . We first examine the case when large and small males are born into the population at the same time-constant rate, but we will later investigate the effect of relaxing this assumption. The number of individuals that occupy rich and poor resources can be described by a dynamic system, which is presented in the Appendix. Here, we briefly describe the dynamic state changes for a large male, and the dynamics is also depicted by Fig. 1.

Single males may acquire a single female (rate: a_{LP} , a_{Lp}). If he already has a female, he may lose her to another individual because of a takeover. This may also mean that the male dies because of injury (survival rate S). Therefore, the rate at which large males become

single again after having lost their female is $S \sum_y u_{yLP}$ and $S \sum_y u_{yLp}$ for high- and low-quality

females, respectively. The male may also become single again when he leaves the female after having completed breeding ($1/T$). This is the only rate that leads to a fitness gain. Besides mortality unrelated to the sexual behaviour, males suffer increased mortality because of failed takeover attempts. This mortality rate is Ω (see Appendix).

Highly and poorly productive females are born at the time-constant rates B_p and B_r . We assume that the overall recruitment of males and females is equal, so that $B_p + B_r = B_L + B_s$. Females of quality P become guarded by individuals of size L at the rate $M_1 n_L q_{LP}$. A guarded female can only become single again when the male leaves her (rate: $1/T$). Because we assume that this rate is constant and identical for all males, takeovers do not change the female dynamics and do not have to be taken into account. Single females die at the rate μ .

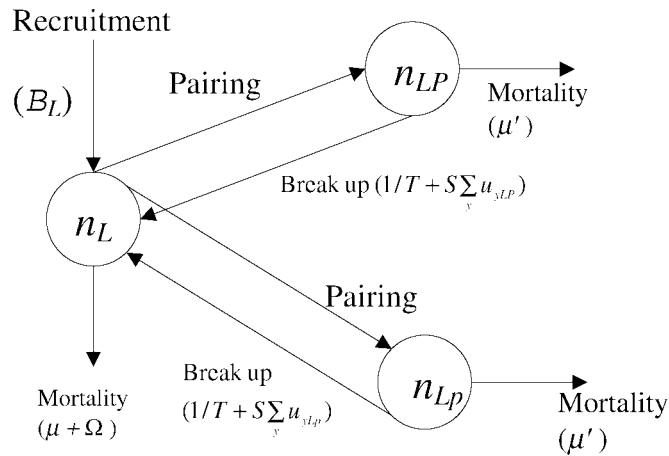


Fig. 1. Path diagram of the dynamics of large males. The symbols in the diagram are explained in the text. The variable Ω is the rate of mortality caused by failed attempts to take over females from other males (see Appendix for explanation).

Each strategy leads to a stable population structure. We use a numeric procedure to compute this stable population state. First, we assume some distribution of female qualities. This enables us to calculate the stable number of bachelors and pairs, using the equation system (A1) in the Appendix. With these values, we can calculate a new distribution of spinsters using equation system (A2). We then go back to (A1) and calculate a new stable number of bachelors and pairs. We continue these iterations until a stable population distribution is reached.

Assortative pairing

For each solution, we calculate the correlation between male and female qualities in pairs as a measure of assortative pairing. The correlation coefficient ρ ($-1 \leq \rho \leq 1$) is calculated from the number of pairs at equilibrium as

$$\rho = \frac{n_{LP}n_{sp} - n_{Lp}n_{sP}}{\sqrt{(n_{LP} + n_{Lp})(n_{sP} + n_{sp})(n_{LP} + n_{sP})(n_{Lp} + n_{sp})}} \tag{7}$$

Recruitment rates

We investigate the effect of differing recruitment rates of high- and low-quality individuals. In the baseline case, all recruitment rates are equal, $B_p = B_p = B_L = B_s$. Second, we assume that small males are recruited into the breeding population at three times the rate of large males, while keeping $B_p = B_p$ for females. We also investigate the converse, letting $3B_p = B_p$.

Mutant fitness

A male’s fitness is proportional to the number of times a male completes a mating with a certain type of female, weighted by the productivity of that female. To derive this quantity, let us focus on a particular male, say a large male. If this individual increases his motivation to usurp poor females occupied by large males, he experiences an increased rate of pair

formation $F_{Lp} + \delta$, compared with F_{Lp} 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 compared with other males in this population. To calculate mutant male fitness at time t , let the fitness gain from a high- and a low-quality female be G_p and G_{lp} , respectively. Sum these, weighted with the probability $\pi_{Lp}(t)$, and $\pi_{Ll}(t)$, that the male is alive at t and has a female of high and low quality, respectively (see Appendix). Multiply with the fitness increase rate, which is proportional to the rate of completion of the reproductive cycle $1/T$. Lifetime fitness W is the integral of this over time, i.e.

$$W = \int_0^{\infty} \pi_{Lp}(t)G_p/T + \pi_{Ll}(t)G_{lp}/T dt \quad (8)$$

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 is as follows: Given the present population strategy J , calculate the stable population structure using (A1–A2). Then for each probability (motivation) q , pick the probability 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

$$J(s+1) = (1-\lambda)J(s) + \lambda I(s) \quad (9)$$

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 only finds one ESS at a time. Starting from different (random) starting strategies, we always found convergence to the same ESS. Thus we did not find multiple equilibria in the game, although we note that our numerical procedure is incapable of proving that no multiple stable solutions exist.

RESULTS

There are a large number of solutions to the evolutionary game. However, all solutions are possible to classify as one of the six solutions (A) to (F) presented in Fig. 2, or as a linear combination of two of the solutions in Fig. 2. A numerical solution was classified as one of the solutions (A) to (F) if none of the probability values in this strategy differed by more than 0.1 from the pure solutions in Fig. 2. Linear combinations of two of the solutions in Fig. 2 were characterized with subscripts denoting the solutions, I_{BC} for combinations of (B) and (C) and so on. We map all solutions onto a parameter space of meeting rate (M), and (S), the survival rate after losing a takeover fight (Figs. 3–5). In each panel of these figures, we present solutions for five meeting rate values (M) from 10 to 1000 column-wise. Each row stands for a value of S from 0 to 1. We assume that $M = M_1 = M_2$. The top row of panels shows the evolutionarily stable male mating strategy under four different values of v_{Ls} (Fig. 3). The bottom row of panels presents the correlation between male and female quality in pairs (ρ) that results when males follow evolutionarily stable mating strategies. The panels thus belong together column-wise.

The solutions differed dependent on the relation between the recruitment rates of large and small males and the recruitment of low- and high-quality females. We will therefore first discuss the case with equal recruitment rates, and then turn to the effect of altering this assumption.

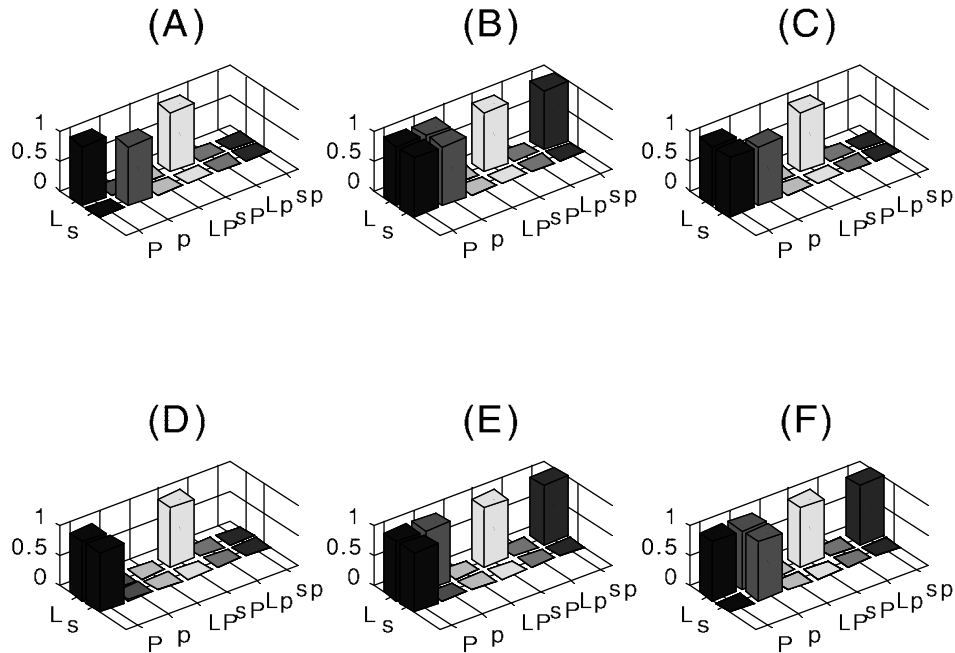


Fig. 2. Six potential ESS solutions of the game. On the x-axis are the different potential female targets. On the y-axis is male quality, large or small. On the z-axis is the probability of a mating attempt (i.e. the q -value; see text). All q -values are either 0 or 1 in these ‘pure’ solutions. For most parameter combinations, the solution was very close to one of these solutions, as presented in Figs. 3–5. Intermediary solutions were possible expressed as linear combinations of two of the six solutions (A)–(F).

Solution (A) in Fig. 2 shows a strategy with marked assortative mating and prudent choice. The height of each bar in the figure shows the ESS probability (i.e. the ESS q) for takeover or mating attempts, and can be 0 or 1 in these cases. On the x-axis, each of the six categories represents a female quality class, single or paired, and on the y-axis are the male size classes. Large males are only attracted to highly productive females, and not to low-quality females. Small males are only attracted to low-quality females. Large males will also attempt to take over highly productive females if these are guarded by small males. Under this strategy, assortative mating is strong, with mainly pairs of large males and high-quality females, and pairs of small males and low-quality females (Fig. 3). In Fig. 3 (case A), this ESS is found with a high meeting rate (M), a high cost of losing takeover fights (low survival, S) and a high probability of successful takeover for large males (v_{L_s}). The ‘opposite’ solution of totally indiscriminate mating (solution (B) in Fig. 2) is favoured by opposite conditions – that is, low M , high S and low v . Under this solution, the correlation between mated male and female qualities is zero (Fig. 3). Large males will in this case take over females from small males, but they do this irrespective of female quality. Large males do not challenge other large males who currently guard a female.

Intermediate between these extremes, we find solutions where only one male class mates indiscriminately. If the meeting rate is high enough, and losing a takeover fight seldom leads to death, we may get solution (C), where small males mate with both types of

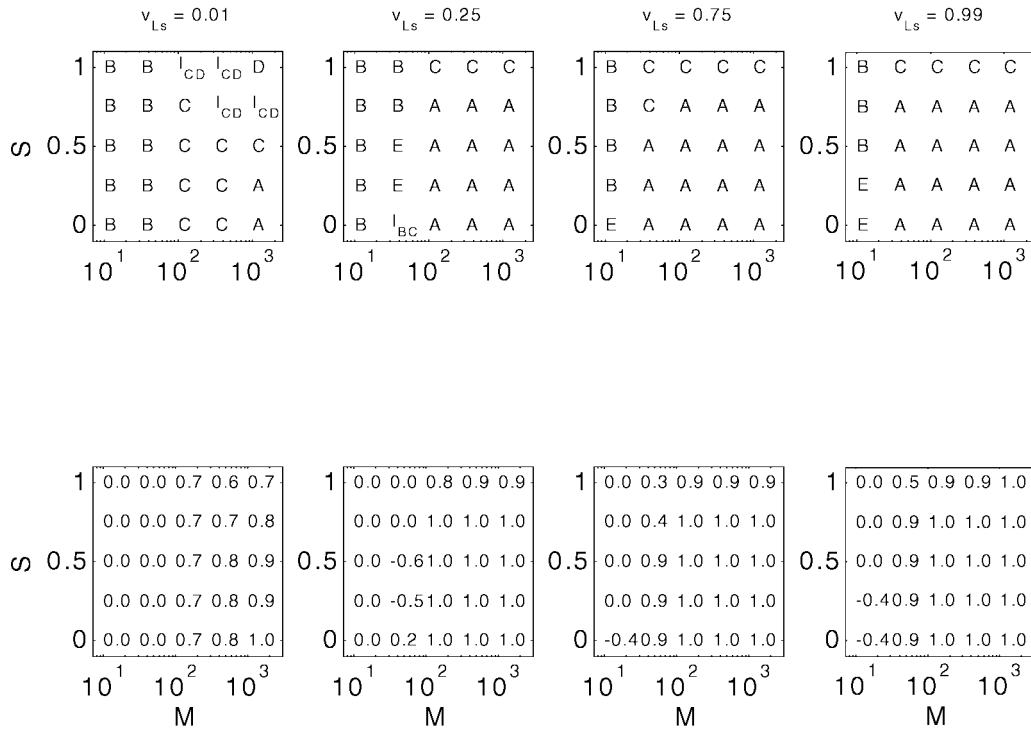


Fig. 3. Each panel shows a parameter space of meeting rate M (assuming $M_1 = M_2$) and survival of takeover fights (S). The top row of panels shows the ESS calculated for all combinations of $M = 10, 31.6, 100, 316.2, 1000$, and $S = 0, 0.25, 0.5, 0.75, 1$, mapped onto this space. The letters in the matrix correspond to a solution in Fig. 2, and solutions intermediate between two solutions in Fig. 2 are denoted I_{CD} and so forth. The four panels are for different values of v_{Ls} as indicated above the panels. The bottom row of panels shows the correlation (equation 7) between male and female quality in pairs formed when the male follows the ESS. The two panels in each column belong together. Other parameters: $T = 0.1, \mu' = 1.2, \mu = 1, B_p = B_p = B_L = B_s = 1$.

females, although large males are only attracted to highly fecund ones (Fig. 3). This solution is also favoured by low values of v_{Ls} , the probability that a large male succeeds in taking over a female from a small male. As before, large males take over high-quality females from small males. This leads to less strong assortative mating than solution (A), although the quality correlation is still positive. In the opposite case, where the meeting rate is low, while takeovers are easy and associated with high risks for the loser, we find an interesting case shown by solution (E). Here large males mate indiscriminately with both types of female, but small males are only attracted to high-quality females. This leads to a negative correlation between male and female quality in pairs. Finally, another possible solution is (D). Here both large and small males mate only with large females, and large males take over large females paired with small males. This occurs if takeover attempts are very seldom successful, losing a takeover fight almost never leads to death, and the meeting rate is so high that males can afford to reject low-quality females completely. In the examples we present (Figs. 3 and 4), any solution will be classified as (D) even if low-quality males still show some attraction towards low-quality females (<10% chance

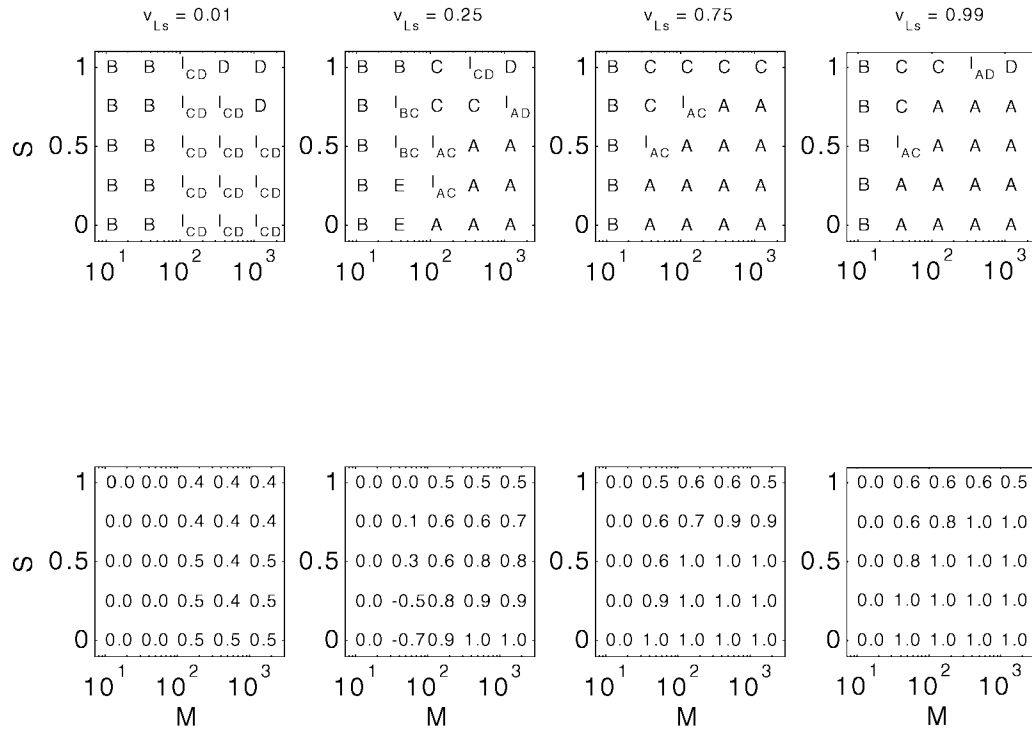


Fig. 4. Same as Fig. 3, except that the recruitment rate of small males is three times as high as that of large males, i.e. $B_p = 1, B_p = 1, B_L = 0.5, B_s = 1.5$. Other parameters: $T = 0.1, \mu' = 1.2, \mu = 1$.

of mating). Therefore, these cases show assortative mating resulting from takeovers by large males.

The model also allows us to investigate the effects of varying population structure. In Fig. 4, we consider a case where most males are small, by assuming that small males are recruited to the population at three times the rate of large males. The effect of reduced competition from large males is that small males become more interested in high-quality females, reflected by an increase in the region where (C) and (D) are solutions (Fig. 4).

In Fig. 5, the population is biased in favour of low-quality females, which are recruited at three times the rate of high-quality females. The competition over high-quality females is therefore increased, and the payoff of only targeting these as partners is small. This increases the region where (B) is an ESS (Fig. 5). In the region intermediate between (A) and (B) there is some increase of solutions which mean that large males target both types of females, such as (E).

DISCUSSION

We have shown that intra-sexual competition over mating partners may have a profound influence on the evolution of mating strategies, and lead to a positive as well as negative correlation between male and female quality in pairs. For males to shift their mating preferences adaptively, the meeting rate of individuals should not be too low. Low meeting

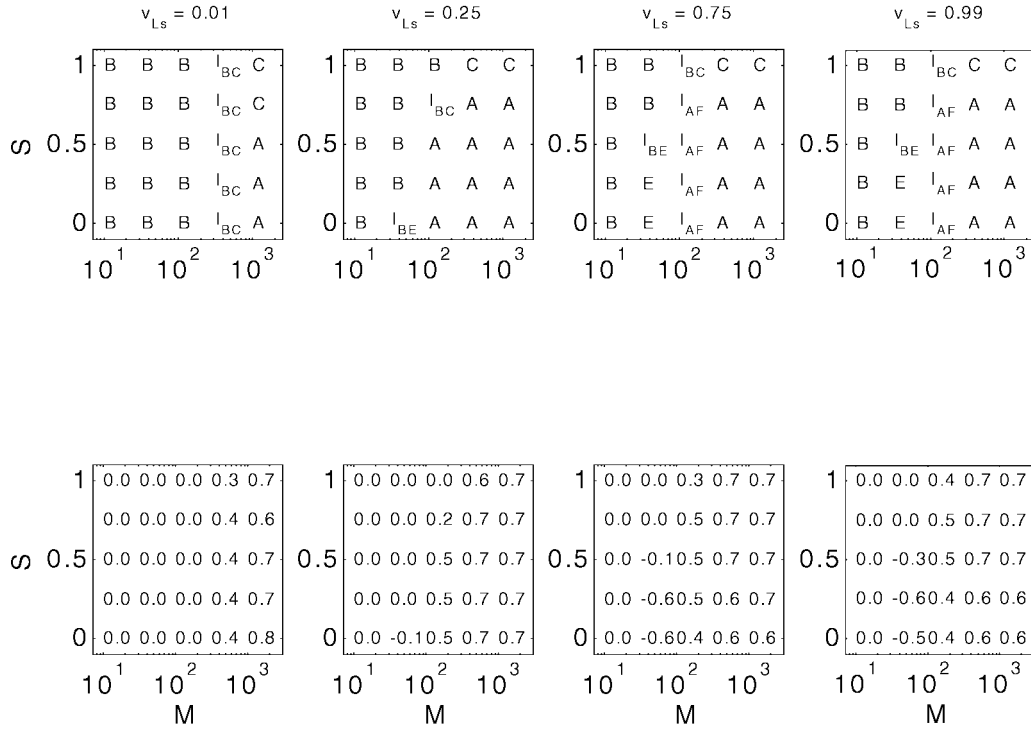


Fig. 5. Same as Fig. 3, except that the recruitment rate of low-quality females is three times as high as that of high-quality females, i.e. $B_p = 0.5$, $B_p = 1.5$, $B_L = 1$, $B_S = 1$. Other parameters: $T = 0.1$, $\mu' = 1.2$, $\mu = 1$.

rates in Figs. 3–5 generally lead to indiscriminate matings by males, yielding a zero male–female quality correlation. This is because low meeting rates (e.g. due to low mobility of the individuals) imply that both high- and low-quality males have problems finding a mate at all. Tactical decisions to reduce costs of competition are therefore of less importance. An additional fact promoting indiscriminate matings in this case is that if a low-quality male finds a mate, and the meeting rate is low, the risk is small that a high-quality male takes over this female before breeding is completed.

When meeting rates are high enough for competition to influence mate preferences, different male strategies evolve dependent on the risk of losing one’s partner due to a takeover and the associated costs. We have chosen to model these costs as only due to takeovers from other males, and let the chosen resource (here, the female) play a passive role. This enables us to extend the conclusions to systems other than mate choice, for example choice of territories where individuals should not always try to possess the best location (see Broom *et al.*, 1997).

It may benefit a male of poor competitive ability to reject mates (or territories) of too high quality, because the costs of trying to keep the mate/territory for a sufficiently long time would be prohibitively high. We will term this solution ‘prudent choice’ (solution (A) in Fig. 2), and this strategy is generally favoured by high meeting rates, a high rate of successful takeovers, and large costs for the loser in takeover fights. This effect can be

surprisingly strong: it is possible to find scenarios where the best females end up being rejected more often than poorer quality females, because the majority of males find targeting these females too costly.

Prudent choice leads to strong assortative pairing in our examples, often close to unity, so that there are no pairs where the sexes have differing quality. It should be noted that some solutions that are classified as (A) in Figs. 3–5 differ slightly from the pure solution in Fig. 2. These cases lead to a somewhat lower (and more realistic) quality correlation.

Relaxing any of the conditions leading to prudent choice gives rise to other stable solutions, with concomitant effects on assortative pairing. Contrast solutions (C) and (E), which are in many senses opposites. They occur in opposite regions of the parameter spaces depicted in Figs. 3–5 and also have opposite effects. With solution (C), there is assortative mating with a positive correlation between qualities. Although small males are equally attracted to both female qualities, large males are only attracted to high-quality females, and also take over high-quality females from small males. The result is a positive correlation between male and female quality in pairs. We find this solution in particular in the parameter space with a low mortality risk for the loser in a takeover fight (high S), and a high meeting rate (Fig. 3). Here, most small males survive losing a high-quality female to a large male. The meeting rate is also high enough to make it worthwhile for large males only to target high-quality females.

In contrast, solution (E) leads to a negative correlation between male and female quality in pairs (Fig. 3–5), because small males only target large females while large males mate indiscriminately (Fig. 2). This ‘paradoxical’ solution is generally found under conditions opposite to those leading to (C) – that is, low meeting rates and high risks for the loser in a takeover fight. The logic behind this solution is that meeting rates are so low that large males cannot afford to target only high-quality females. A large male that did would suffer a too high cost of lost mating opportunity, which is also why large males usurp females of any quality from small males. In this situation, small males suffer as high a risk of partner loss independent of the quality of their female. Partner loss also usually spells the end of a male’s life. Thus mating is highly risky for small males in solution (E), and a ‘desperado’ strategy (*sensu* Grafen, 1987) is then expected to evolve: low-quality males may get lucky if they can sometimes complete mating before a large male arrives and takes over the female. Because large males take over both high- and low-quality females from small males, the latter do best by aiming high, as this is their only chance of gaining fitness. Highly costly mating attempts generally increase choosiness in males, which helps to explain choosiness in this case despite the rarity of available females (see Kokko and Monaghan, 2001).

In a population where males use strategy (D), only high-quality females are targeted by males, and low-quality females are rejected; this solution resembles sex role reversal. This solution appears under higher meeting rates than those leading to solution (C) (Figs. 3–5). Intuitively, very high meeting rates in combination with low risks connected with takeovers make it beneficial for both large and small males to target only high-quality females. If a small male loses one partner, he will soon find another. Assortative pairing should not result from this strategy, but solution (D) does not occur as a pure game solution in the examples depicted here. Because small males are (a little) attracted to low-quality females, the quality correlation between males and females is higher than zero. Finally, although a solution like (F) might lead to weak assortative pairing, this solution was only found as part of a linear

combination with (A), thus it is difficult to assess the conditions which would favour this solution.

In Fig. 4, the recruitment rate of small males is three times that of large males, so that the population is biased in favour of small males. This may reflect the case where male growth is indeterminate, and older males survive between seasons with some probability; alternatively, strong competitors may simply be rare from the start. The general effect of this is to increase the areas where (C) is a solution (Fig. 4). Solution (D) is also favoured, and both these solutions mean that small males become more interested in high-quality females. This is because of the lowered threat experienced by small males. Because there are fewer large males around, the risk that they usurp large females is lowered, and small males can then afford to mate more indiscriminately, and focus almost completely on high-quality females.

In Fig. 5, low-quality females are recruited at three times the rate of high-quality females, which could similarly depend on indeterminate growth in combination with between-year survival. This increases the region where (B) is an ESS (Fig. 5). Large males cannot here afford to target only high-quality females, and must mate more indiscriminately. If large males do this, low-quality females are no longer a safe choice for small males, so they must also mate indiscriminately, which leads to solution (B). In the region intermediate between (A) and (B) there is some increase of solutions, which means that large males target both types of females, such as in (E).

Some of our results are in line with those of Fawcett and Johnstone (2003), who modelled the evolution of mate preferences during a pre-breeding period of mate acquisition. They found that the evolutionarily stable strategy early in the mate acquisition period may show a tendency for what we here call 'prudent choice'. In our terminology, this is a solution intermediate between (A) and (C). Later, poor competitors increase their preference for high-quality partners, so that the solution is intermediate between (C) and (D), in our terms. Very close to the start of breeding, males become indifferent (cf. solution (B)). These differences arise because of the assumption of a fixed time horizon. The time until the start of the breeding season automatically influences both the probability of acquiring a mate and the probability of being able to defend a mate from usurping males until the deadline. In our more general model, this effect of the finite time horizon can be mimicked by reducing the meeting rate (M). Reducing M leads to an increased risk of not finding a partner and a lower risk of partner loss because of a takeover, just as with an approaching time horizon. In Fig. 3, for example, decreasing M may shift the solution from (A) to (C) and finally (B), which is in rough correspondence with the results of Fawcett and Johnstone (2003).

Are our results generally applicable? Any model makes assumptions, and it is instructive to consider possibilities to relax them. For example, in the context of mate choice, the 'resource' may not be passive but may respond to male quality: if a female can sequentially choose males such that she may switch to a higher quality male than her current partner (Simao and Todd, 2002), a male who 'aims too high' may end up not gaining fitness from his current mating attempt. We would then expect similar assortative-pairing patterns to emerge as in the current model, and further work is required to determine how such a scenario differs from the current one. It is possible that divorce initiated by the opposite sex is a smaller cost than the potentially life-threatening male–male contests that our model is based on. Therefore, discrimination against too high-quality mates is potentially milder in cases of sequential mate choice and divorce than in our case, although the essence of the argument is the same.

In other settings, however, further work is required to examine the probable course of evolution. Consider, for example, that the cost of occupying a high-quality resource item is not risk of injury (as in the current model) or a risk of being rejected (as in cases of divorce initiated by females), but the time it takes to establish ownership of the resource. As an example, females could require a certain period of courtship feeding before they accept a mate. While the expected benefits from courtship feeding probably increase with male quality in this setting (as the female is more likely to be impressed by a high feeding rate), the costs of this behaviour may either decrease or increase with quality. A decrease is expected if finding items to feed to the female is easier for the high-quality male. But if the high-quality male has better prospects of mating success in general, the lost opportunity costs of spending time on one particular female increase with male quality. Thus it is possible that both benefits and costs increase with quality, which means that their balance can shift in either direction. Clearly, male and female strategies to find the highest quality mate will co-evolve in such a setting, and whether and how assortative mating and/or prudent choice emerges in such cases is a matter for further study.

It is well known that male–male competition in combination with male choice can result in assortative mating. This occurs in taxa as different as isopods (e.g. Ridley and Thompson, 1979), anurans (Arak, 1983) and coleopterans (McLain and Boromisa, 1987). However, the kind of evolution predicted by our model, where mate preferences are formed by costs of male–male competition, is not often reported. One species in which it occurs is garter snakes (*Thamnopsis sirtalis parietalis*), where males select mates actively and choice is also size dependent so that large males only court large females, while small males are much less discriminating (Shine *et al.*, 2001). The reason is that large males are much better at competing for the large females, so that small males do better by focusing on the small females instead (Shine *et al.*, 2001, 2003, 2004).

In the marine isopod *Idotea baltica*, males are only attracted to females that have reached a certain point in their moulting cycle, because females are only receptive during a few hours after they have moulted. In a study by Jormalainen *et al.* (2000), the male criterion for targeting and guarding females was shown to be plastic and related to the males' experience of the competitive situation. Large males that were kept with a small male delayed their guarding criterion compared with large males that were kept with a female. It is possible that the presence of the smaller male made large males perceive themselves as competitively superior and in a position to take over females from other males (Jormalainen *et al.*, 2000). This may have caused them to focus on more mature and valuable females.

In the two-spotted goby *Gobiusculus flavescens*, small males have been shown to be unselective, while large males prefer more colourful females as mates (Amundsen and Forsgren, 2003). Small males in this species probably run the risk of having their territories taken over by large males, which explains their mating behaviour.

Finally, earthworms (*Lumbricus terrestris*) are hermaphrodites, but it is possible that they still show partner choice. Michiels *et al.* (2001) demonstrated size assortativeness in one of two samples of mating earthworms. Also, in partner choice experiments the waiting time until copulation was shorter with a similar-sized partner, although the sample size was small. A possible cost connected with mating with too big a partner is that the bigger and stronger partner will pull the small one out of its burrow after mating, leaving the small individual unprotected on the ground (Michiels *et al.*, 2001).

The above evidence notwithstanding, much more empirical work is needed to evaluate the possibility that mate preferences are shaped by competition for mates in addition to direct

and indirect benefits of adaptive mate choice (Andersson, 1994). The model presented here is a contribution to this end, as it outlines the conditions under which different mate choice strategies are expected to be evolutionarily stable. We do not know, however, how often prudent choice (or, indeed, its counterpart of ‘paradoxical’ negative assortative mating) occurs in nature, if it often underlies assortative mating patterns, or what the adaptive consequences of such behaviour are. Given the strong implications for the evolution of mating systems – even leading to the highest quality mates being ignored in some cases – we certainly encourage further research in this area.

ACKNOWLEDGEMENTS

We would like to thank Anders Brodin, Jonathan Wright and an anonymous referee for providing helpful comments. We also wish to thank the Swedish Research Council (R.H.) and the Academy of Finland (H.K.) for funding.

REFERENCES

- Alatalo, R.V., Höglund, J., Lundberg, A. and Sutherland, W.J. 1992. Evolution of black grouse leks: female preferences benefit males in larger leks. *Behav. Ecol.*, **3**: 53–59.
- Amundsen, T. and Forsgren, E. 2001. Male mate choice selects for female coloration in a fish. *Proc. Natl. Acad. Sci. USA*, **98**: 13155–13160.
- Amundsen, T. and Forsgren, E. 2003. Male preference for colorful females affected by male size in a marine fish. *Behav. Ecol. Sociobiol.*, **54**: 55–64.
- Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Andersson, S., Ornborg, J. and Andersson, M. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proc. R. Soc. Lond. B*, **265**: 445–450.
- Arak, A. 1983. Sexual selection by male–male competition in natterjack toad choruses. *Nature*, **306**: 261–262.
- Bergstrom, C.T. and Real, L.A. 2000. Towards a theory of mutual mate choice: lessons from two-sided matching. *Evol. Ecol. Res.*, **2**: 493–508.
- Black, J.M. and Owen, M. 1995. Reproductive performance and assortative pairing in relation to age in barnacle geese. *J. Anim. Ecol.*, **64**: 234–244.
- Bonduriansky, R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.*, **76**: 305–339.
- Broom, M., Cannings, C. and Vickers, G.T. 1997. A sequential-arrivals model of territory acquisition. *J. Theor. Biol.*, **189**: 257–272.
- Buston, P.M. and Emlen, S.T. 2003. Cognitive processes underlying human mate choice: the relationship between self-perception and mate preference in Western society. *Proc. Natl. Acad. Sci. USA*, **100**: 8805–8810.
- Craig, A.S. 2002. Male mate choice and male–male competition coexist in the humpback whale (*Megaptera novaeangliae*). *Can. J. Zool.*, **80**: 745–755.
- Crespi, B.J. 1989. Causes of assortative mating in arthropods. *Anim. Behav.*, **38**: 980–1000.
- Fawcett, T. and Johnstone, R.A. 2003. Mate choice in the face of costly competition. *Behav. Ecol.*, **14**: 771–779.
- Ferrer, M. and Penteriani, V. 2003. A process of pair formation leading to assortative mating: passive age-assortative mating by habitat heterogeneity. *Anim. Behav.*, **66**: 137–143.
- Grafen, A. 1987. The logic of asymmetric contests: respect for ownership and the desperado effect. *Anim. Behav.*, **35**: 462–467.
- Härdling, R., Kokko, H. and Elwood, R.W. 2004. Priority versus brute force: when should males begin guarding resources? *Am. Nat.*, **163**: 240–252.

- Hedge, S.N. and Krishna, M.S. 1997. Size-assortative mating in *Drosophila malerkotliana*. *Anim. Behav.*, **54**: 419–426.
- Houston, A.I. and McNamara, J.M. 1999. *Models of Adaptive Behaviour: An Approach Based on State*. Cambridge: Cambridge University Press.
- Houston, A.I. and McNamara, J.M. 2002. A self-consistent approach to paternity and parental effort. *Phil. Trans. R. Soc. Lond. B*, **357**: 351–362.
- Itzkowitz, M. and Haley, M. 1999. Are males with more attractive resources more selective in their mate preferences? A test in a polygynous species. *Behav. Ecol.*, **10**: 366–371.
- Jennions, M.D. and Petrie, M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol. Rev.*, **72**: 283–327.
- Johnstone, R.A. 1997. The tactics of mutual mate choice and competitive search. *Behav. Ecol. Sociobiol.*, **40**: 51–59.
- Johnstone, R.A., Reynolds, J.D. and Deutsch, J.C. 1996. Mutual mate choice and sex differences in choosiness. *Evolution*, **50**: 1382–1391.
- Jormalainen, V., Merilaita, S. and Härdling, R. 2000. Dynamics of intersexual conflict over precopulatory mate guarding in two populations of the isopod *Idotea baltica*. *Anim. Behav.*, **60**: 85–93.
- Kalick, S.M. and Hamilton, T.E. 1986. The matching hypothesis reexamined. *J. Personality Soc. Psych.*, **51**: 673–682.
- Kirkpatrick, M., Price, T. and Arnold, S.J. 1990. The Darwin–Fisher theory of sexual selection in monogamous birds. *Evolution*, **44**: 180–193.
- Kokko, H. and Monaghan, P. 2001. Predicting the direction of sexual selection. *Ecol. Lett.*, **4**: 159–165.
- McLain, D.K. and Boromisa, R.D. 1987. Male choice, fighting ability, assortative mating and the intensity of sexual selection in the milkweed longhorn beetle *Tetraopes tetraophthalmus* (Coleoptera, Cerambycidae). *Behav. Ecol. Sociobiol.*, **20**: 239–246.
- McNamara, J.M. and Collins, E.J. 1990. The job search problem as an employer-candidate game. *J. Appl. Prob.*, **28**: 815–827.
- Michiels, N.K., Hohner, A. and Vorndran, I.C. 2001. Precopulatory mate assessment in relation to body size in the earthworm *Lumbricus terrestris*: avoidance of dangerous liaisons? *Behav. Ecol.*, **12**: 612–618.
- Motro, U. 1994. Evolutionary and continuous stability in asymmetric games with continuous strategy sets: the parental investment conflict as an example. *Am. Nat.*, **144**: 229–241.
- Parker, G.A. 1983. Mate quality and mating decisions. In *Mate Choice* (P. Bateson, ed.), pp. 141–166. Cambridge: Cambridge University Press.
- Parker, G.A. and Sutherland, W.J. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim. Behav.*, **34**: 1222–1242.
- Preston, B.T., Stevenson, I.R. and Wilson, K. 2003. Soay rams target reproductive activity towards promiscuous females' optimal insemination period. *Proc. R. Soc. Lond. B*, **270**: 2073–2078.
- Priest, R.F. and Thein, M.T. 2003. Humor appreciation in marriage: spousal similarity, assortative mating, and disaffection. *Humor – Int. J. Humor Res.*, **16**: 63–78.
- Reinhold, K., Kurtz, J. and Engqvist, L. 2002. Cryptic male choice: sperm allocation strategies when female quality varies. *J. Evol. Biol.*, **15**: 201–209.
- Ridley, M. and Thompson, D.J. 1979. Size and mating in *Asellus aquaticus* (Crustacea, Isopoda). *Z. Tierpsychol.*, **1979**: 380–397.
- Riechert, S.E. and Singer, F.D. 1995. Investigation of potential male mate choice in a monogamous spider. *Anim. Behav.*, **49**: 715–723.
- Rintamaki, P.T., Lundberg, A., Alatalo, R.V. and Höglund, J. 1998. Assortative mating and female clutch investment in black grouse. *Anim. Behav.*, **56**: 1399–1403.
- Saether, S.A., Fiske, P. and Kålås, J.A. 2001. Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird. *Proc. R. Soc. Lond. B*, **268**: 2097–2102.

- Shine, R., Olsson, M.M., Moore, I.T. *et al.* 2000. Body size enhances mating success in male garter snakes. *Anim. Behav.*, **59**: F4–F11.
- Shine, R., O'Connor, D., LeMaster, M.P. and Mason, R.T. 2001. Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. *Anim. Behav.*, **61**: 1133–1141.
- Shine, R., Phillips, B., Wayne, H., LeMaster, M. and Mason, R.T. 2003. The lexicon of love: what causes size-assortative courtship by male garter snakes? *Behav. Ecol. Sociobiol.*, **53**: 234–237.
- Shine, R., Langkilde, T. and Mason, R.T. 2004. Courtship tactics in garter snakes: how do a male's morphology and behaviour influence his mating success? *Anim. Behav.*, **67**: 477–483.
- Simao, J. and Todd, P.M. 2002. Modeling mate choice in monogamous mating systems with courtship. *J. Adaptive Behav.*, **10**: 113–136.
- Sutherland, W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Sutherland, W.J. and Parker, G.A. 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Anim. Behav.*, **44**: 345–355.
- Webb, J.N., Houston, A.I., McNamara, J.M. and Székely, T. 1999. Multiple patterns of parental care. *Anim. Behav.*, **58**: 983–993.
- Wedell, N., Gage, M.J.G. and Parker, G.A. 2002. Sperm competition, male prudence and sperm-limited females. *Trends Ecol. Evol.*, **17**: 313–320.

APPENDIX

Male and female dynamics

Here we present the dynamic systems for the number of single and paired individuals of different male size classes (Fig. 1). Large males are born into the population at the rate B_L and small males at the rate B_s . We assume that females may be either productive (P) or poor (p). The dynamics for large males is given by:

$$\begin{aligned}
 &(-\mu - F_{LP} - F_{Lp} - \Omega)n_L + \\
 &+ S \sum_y u_{yLP}n_{LP} + S \sum_y u_{yLp}n_{Lp} = -B_L \\
 &F_{LP}n_L - D_{LP}n_{LP} = 0 \\
 &F_{Lp}n_L - D_{Lp}n_{Lp} = 0
 \end{aligned} \tag{A1}$$

where D is calculated according to equation (6). Ω holds the rate of mortality created by failed takeover attempts, $\Omega = (M_2n_{LP}q_{LLP} + M_2n_{Lp}q_{LLp})(1 - v_{LL})(1 - S) + (M_2n_{sP}q_{LsP} + M_2n_{sp}q_{Lsp})(1 - v_{Ls})(1 - S)$. An equivalent system holds for the small male size class.

The female reproductive cycle is completed by the reproductive moult. After the reproductive moult, the female is again single. The dynamics for females is explained in the text. The dynamic system for the distribution of productive females is:

$$\begin{aligned}
 &(-\mu - F_{LP} - F_{sP})n_P + n_{sP}T + n_{LP}T = -B_P \\
 &F_{sP}n_s - D_{sP}n_{sP} = 0 \\
 &F_{LP}n_L - D_{LP}n_{LP} = 0
 \end{aligned} \tag{A2}$$

An equivalent system holds for low-quality females. 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. Together, (A1) and (A2) define the equilibrium densities of males, females, and all possible types of pairs, under a given male strategy.

Mutant fitness

Now we focus on a mutant male belonging to the class s . The mutant has a different strategy than the other small males in the population. This difference is reflected in the rate of pair formation F , where the mutant uses F' instead of the population average. 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 determine if the mutant male strategy will be able to invade the resident population strategy, we need to know the probability $\pi_L(t)$ that the male using the strategy is alive and single at time t , and for female qualities x the probability $\pi_{Lx}(t)$ 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:

$$\begin{aligned}
 &(-\mu - F_{LP} - F_{Lp} - \Omega)\pi_L(t) + \\
 &+ S \sum_y u_{yLP}\pi_{Lp}(t) + S \sum_y u_{yLp}\pi_{LP}(t) = 0 \\
 &F_{Lp}\pi_L(t) - D_{Lp}\pi_{Lp}(t) = 0 \\
 &F_{LP}\pi_L(t) - D_{LP}\pi_{LP}(t) = 0 \\
 &\{\pi_L(0) = 1, \pi_{Lp}(0) = 0, \pi_{LP}(0) = 0\}
 \end{aligned} \tag{A3}$$

The initial condition arises from the fact that a male is single when entering the population, thus $\pi_L(0) = 1$. Mutant male fitness at time t is the probability that the mutant male is alive and has a female, multiplied by the female's rate of completion of the reproductive cycle $1/T$ times the fitness increase rate G_x , which depends on the female quality x . Lifetime fitness W is the integral of this over time, i.e.

$$W = \int_0^\infty (\pi_p(t)G_p/T + \pi_p(t)G_p'/T)dt \tag{A4}$$

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:

$$\begin{aligned}
 &(-\mu - F_{LP} - F_{Lp} - \Omega)\Delta\pi_L + \\
 &+ S \sum_{y=L,s} u_{yLP}\Delta\pi_{Lp}(t) + S \sum_{y=L,s} u_{yLp}\Delta\pi_{LP}(t) = -1 \\
 &F_{Lp} \Delta\pi_L(t) - D_{Lp} \Delta\pi_{Lp}(t) = 0 \\
 &F_{LP} \Delta\pi_{SL}(t) - D_{LP} \Delta\pi_{LP}(t) = 0
 \end{aligned} \tag{A5}$$

where $\Delta\pi_i(t) = \int_0^\infty \pi_i(t)dt$. This solution enables us to calculate the fitness of the mutant.

