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Mate choice in the face of costly competition

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Studies of mate choice commonly ignore variation in preferences and assume that all individuals should favor the highest-quality mate available. However, individuals may differ in their mate preferences according to their own age, experience, size, or genotype. In the present study, we highlight another simple reason why preferences may differ: if there is costly competition for mates, the poorest competitors might be better off avoiding the highest-quality partners and instead targeting low-quality partners, so that they minimize the costs they incur. We present a game-theoretical model of mate choice in which males of differing quality compete for access to females and try to retain them till the time of mating. Our model predicts that high-quality males, who are better competitors, have a preference for the best females that is typically several times stronger than that of low-quality males. Early in the competitive period, the latter may even prefer low-quality females over high-quality females. Thus, variation in competitive ability generates variation in both the strength and direction of preferences. Differences in competitive ability result in assortative mating with respect to quality, which is reinforced by variation in preferences. As the time of mating draws near and there is an increased risk of ending up unpaired, all males become indifferent to the quality of potential mates. Our findings are equally applicable to female choice for males, and offer a new explanation for adaptive variation in mating preferences based on differing abilities to cope with the costs of mate choice. *Key words:* choosiness, condition-dependent preferences, costly competition, dynamic game, evolutionarily stable strategy, mate choice, preference function. *[Behav Ecol 14: 771–779 (2003)]*

A tacit assumption in studies of mate choice, both empirical and theoretical, is that individuals should strive for the highest-quality mate available. Mate-choice tests in the laboratory are preoccupied with identifying the average preference of a group of animals as a whole, often presupposing that any variation among individuals is "noise" obscuring the overall preference. Recently, however, researchers have begun to address the possibility that different individuals may make different mate-choice decisions for adaptive reasons (for review, see Jennions and Petrie, 1997).

Choosiness over mates is expected to yield benefits by increasing the chances of pairing with a desirable partner, but it may also carry costs in terms of time, energy, and heightened risk of predation (Reynolds and Gross, 1990). The magnitude of these costs and benefits may differ between individuals according to their condition, generating variation in the optimal cost-benefit trade-off (Höglund and Alatalo, 1995) and thereby leading to differences in choosiness (the effort invested in mate assessment) and preference functions (the order in which prospective mates are ranked) (Brooks and Endler, 2001; Jennions and Petrie, 1997).

One type of cost that may differ between individuals is that resulting from competition for mates. In populations in which there is strong competition for mates and in which individuals in good condition are better able to withstand the costs of this competition, lower-quality individuals might do better to settle for a low-quality partner. There are several reasons why pairing with high-quality mates might entail costs as well as benefits (see Jennions and Petrie, 1997; Qvarnström and Forsgren, 1998), and for low-quality individuals, the costs of defending the most sought-after mates might be so great as to make low-quality mates a more attractive option.

This is particularly apparent for species in which contests over mates frequently involve fighting. For example, a young red deer (*Cervus elaphus*) stag who has poor fighting ability might be better off avoiding the healthiest, top-quality hinds because of the injuries he could incur in trying to defend them against other males. Fighting is severe in a wide range of taxa and can occasionally be lethal (e.g., arachnids: Austad, 1983; cervids: Clutton-Brock, 1982; insects: Hamilton, 1979; anurans: Wells, 1977). Besides any risk of injury, fights may also entail high energetic costs (Rand and Rand, 1976; Riechert, 1978) or increase predation risk (Brick, 1998; Cooper, 1999). Fighting and other competition over mates is not restricted to males; between females, competition can also be extremely intense and potentially costly, even in species without sex-role reversal (Brø-Jorgensen, 2002; Dale and Slagsvold, 1995; Petrie et al., 1992; Sæther et al., 2001; Verrell and Brown, 1993).

To investigate how this affects mate preferences, we constructed a model of mate choice in the face of costly competition. We analyzed the problem in terms of males competing for females, but our results apply equally well to female competition over males. Our model took the form of a dynamic game (Clark and Mangel, 2000; Houston and McNamara, 1999; Mangel and Clark, 1988), in which the consequences of an individual's actions depend critically on the behavior of others. We modeled a population composed of high-quality and low-quality individuals, in which males compete for access to females during a mate-acquisition period, and try to retain them till the end of this period when mating occurs. Such mate guarding before copulation is common in a range of taxa (e.g., birds: Birkhead and Møller, 1992; primates: Dixson, 1998; insects: Simmons, 2001). Our basic approach was to track the frequencies of individuals in different states over time and identify the optimal mate-choice strategy in response to this. By repeatedly updating the population strategy and recalculating its best response, we converged on an evolutionarily stable solution.

Our main prediction was that if competition for mates is sufficiently costly, and high-quality males have enough of a competitive advantage over low-quality males, then low-quality males will show a much weaker preference for high-quality

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females and in some circumstances may even prefer low-quality females. This should lead to assortative mating with respect to quality. We also predicted that the choosiness of both types of male would decline toward the end of the mate-acquisition period, as the risk of ending up without a partner increases.

THE MODEL

Outline of the model

The program was written in Pascal and compiled and run by using the software package Codewarrior, version 1.6 (Metrowerks, 1996) on a Macintosh computer.

The population in our model is composed of males and females of high and low quality. To simplify the mathematics, the mate-acquisition period is divided into a series of T discrete time steps. Males will gain a fitness pay-off if they are paired to a female in the final time step, $t = T$. At the start ($t = 1$), all individuals are unpaired. The males are randomly allocated to females—with the condition that no two males can be allocated to the same female—and each is then faced with the decision of whether to stay with his partner or not. Those accepting the female will start the next time step ($t = 2$) paired with her and will not be allocated to another female; those rejecting her will become unpaired and will be reallocated during time step 2.

The allocation process in time step 2 is the same, in that it is essentially random but no male is allocated to the same female as any other unpaired male. However, some of the females may now be paired to a male from the previous time step. A male allocated to a female who is already paired must weigh up the costs and benefits of challenging her partner versus retreating; if he challenges there is a chance that he may win the female, but he also runs the risk of being beaten and suffering a cost, c_{fight}. If he is of higher quality than the paired male, he has a greater chance of winning the contest, but this may be offset by his opponent's advantage in being the established "guarding" male. The guarding male also has a decision to make: he can either fight to keep his mate (with a risk of losing her and incurring cost c_{fight}), or abandon her and suffer a cost, c_{flee}, as the challenger chases him off. Even if he has no challenger, he can still decide to leave his female and search for an alternative mate. All of these decisions and any ensuing contests take place before the start of the following time step.

Subsequent time steps follow a similar pattern. There are two points in each time step that are of special significance in our model: the start of the time step and the "decision point." At the start of time step t, some males are paired and some are unpaired. Unpaired males are then randomly allocated to females, some of which will already be paired to other males. At the decision point, each male decides whether he wants to keep the female or not. These decisions are then executed and any resulting contests are carried out, such that at the start of the following time step, $t + 1$, some males are paired, some are unpaired, and there are no rival males present.

Males make their mate-choice decisions on the basis of their own quality, the quality of the female, the quality of any rival male that is present, and whether they are the guarding male or the challenger. Their decisions affect the chances of having a mate at future time steps. At the end of the mate-acquisition period, defined as the start of time step T, males mate and get a fitness pay-off related to the quality of the female they are with.

Male strategies

A strategy specifies the probabilities that a male will accept a given female for each possible situation he can find himself in at each of the decision points. Each acceptance probability, p, corresponds to a different combination of female quality (low or high), rival quality (absent, low or high), the focal male's own quality (low or high), his "status" (challenger or guarding male), and the time step (1 to $T - 1$; there are no probabilities for time step T because this is the final time step and there are no decisions to be made). We can write this as $p(t,q_m,q_f,q_r,s)$, where t is the time step, q_m is the male's quality, q_f is the female's quality, q_r is the quality of a rival male if one is present, and s is the focal male's status. q_m, q_f, and q_r are integers taking a value of one for a low-quality individual and two for a high-quality individual; if there is no rival male, $q_r = 0$. The status variable takes a value of $s = 0$ if the focal male has been newly allocated to the female, and $s = 1$ if he is already paired to her (i.e., he is the guarding male). Thus, $p(T - 13,1,1,0,1)$ is the probability that a paired low-quality male will remain with a low-quality female at time step $T - 13$, $p(T - 3,2,2,1,0)$ is the probability that an unpaired high-quality male will accept (i.e. be willing to compete for) a high-quality female already paired to a low-quality partner at time step $T - 3$, and so on.

If the acceptance probability of a male of q_m in a given situation is $p(t,q_m,q_f,q_r,s)$, that of a rival playing the same strategy will be $p(t,q_r,q_f,q_m,1 - s)$.

Finding the ESS

Our aim was to find the evolutionarily stable strategy (ESS; Maynard Smith, 1982)—the strategy that, when adopted by all males in the population, cannot be bettered by any rare, mutant strategy. Starting from an arbitrarily chosen population strategy, we identified the ESS by a process of iteration (for an outline of this method, see Houston and McNamara, 1999). The starting strategy we used was one of random choice, in which all acceptance probabilities were set to 0.5, but the values used did not affect the final outcome. The basic procedure involved (1) calculating the frequencies of males and females in different situations resulting from the current population strategy, (2) identifying the best response to this population strategy, (3) updating the population strategy for the next iteration by using a damped best-response procedure (see below), and (4) repeating steps 1–3 until the process converged on a stable solution. The process was halted when a best-response strategy was found that differed from its predecessor by no more than 0.00001 in any of its acceptance probabilities. This was taken to be the ESS.

The equation we used to update the population strategy was

$$\pi_{n+1} = (1 - \lambda)\pi_n + \lambda\hat{b}(\pi_n) \tag{1}$$

where π_{n+1} represents the probabilities of the population strategy used in the $(n + 1)$th iteration and π_n is those of its predecessor, $\hat{b}(\pi_n)$ is the best response to π_n (calculated as described below), and λ is a constant between zero and one controlling the degree to which the population strategy was updated in the direction of its best response. With λ set to zero the new population strategy would be identical to the old one, whereas with λ set to one it would be identical to the best response. In this study we used $\lambda = 0.1$, a value that allowed rapid convergence on the ESS.

Calculating the expected frequencies

Based on the current population strategy, we calculated the expected frequencies of individuals in all possible situations at the start of each time step and at each decision point. This was done in a stepwise process, beginning with the initial frequencies of unpaired males and females of high and low quality at the start of time step 1, using these to calculate the expected frequencies at the decision point, and using the decision-point frequencies in turn to calculate the expected frequencies at the start of time step 2. We could then use these frequencies to calculate the frequencies at the next decision point, and so on. Details of our calculations are given in Appendix A.

None of the females were being guarded by a male in time step 1, but in all subsequent time steps, the expected frequencies were affected by the outcome of fights. We modeled fights as a hawk-dove game (Maynard Smith, 1982), with the winning probability, v, of a q_m male against a q_r rival calculated as

$$v(q_m, q_r) = \frac{1 + h\left(\dfrac{(q_m - q_r)a_{\text{qual}} + (2s - 1)a_{\text{status}}}{a_{\text{qual}} + a_{\text{status}}}\right)}{2} \qquad (2)$$

where a_{qual} is the advantage to a high-quality male when fighting a low-quality male, a_{status} is the fighting advantage to a guarding male over his challenger, and h is the maximum advantage a male can have in a fight (where $0 \leq h \leq 1$). Thus, the chance of winning for a high-quality guarding male fighting a low-quality challenger will be $(1 + h)/2$, whereas for his rival it will be $(1 - h)/2$. Winning probabilities for more even matches are calculated in the same way.

Finding the error-prone best-response strategy

We can write the fitness, or expected pay-off, of a male in a given situation as a function $W(t,q_m,q_f,q_r,s)$, where t, q_m, q_f, q_r, and s are as defined earlier. The best-response strategy is one that, at every decision point, chooses whichever option (accept or reject) gives the greatest value of W. All such fitness values are calculated by working backward from the start of the final time step, $t = T$, when males receive a pay-off, $W_{\text{start}}(T,q_f)$, according to the quality of the female they are with. This is given by

$$W_{\text{start}}(T, q_f) = (q_f/2) \times k \qquad (3)$$

where W_{start} is the male's fitness at the start of the time step, q_f is the female's quality, and k is a constant controlling the difference in pay-off for being paired to a high-quality versus a low-quality female. At the end-point, the variables q_m, q_r, and s are irrelevant because no further contests will take place.

Working backward from this point by using an iterative procedure, outlined in Appendix B, we were able to calculate the fitness consequences of accepting or rejecting a given female in every possible situation at each decision point. Clearly, a male playing the best-response strategy should choose the more favorable of the two options with a probability of one. However, animals are expected to show some error when making decisions (e.g., it may be difficult to assess accurately the quality of the female and any rival that is present). The way we model this error (after McNamara et al., 1997) is based on the assumption that costly mistakes are rarer than cheap mistakes; thus, the bigger the difference between the fitness consequences of accepting a female and rejecting her, the smaller the error in the male's decision making.

For a situation in which accepting the female is the best option, the acceptance probability of the error-prone best-response strategy is given by

$$p' = \frac{1}{\exp\left(\frac{1}{b}(W_{\text{reject}} - W_{\text{accept}})\right) + 1} \qquad (4)$$

where W_{accept} and W_{reject} are the fitness consequences of accepting and rejecting the female respectively, and b is an error constant controlling how prone the animals are to making mistakes. If, on the other hand, rejecting her is the best option, the acceptance probability is

$$p' = \frac{\exp\left(\frac{1}{b}(W_{\text{accept}} - W_{\text{reject}})\right)}{1 + \exp\left(\frac{1}{b}(W_{\text{accept}} - W_{\text{reject}})\right)}. \qquad (5)$$

The set of acceptance probabilities calculated in this way, covering every possible situation at each decision point, is the error-prone best-response strategy: given that animals are likely to make mistakes, it is the strategy giving the greatest pay-off when playing against the current population strategy.

RESULTS

We used a value of $T = 18$ in all our calculations. For the other parameters, except for when they were being manipulated, the default values used were as follows: $k = 10$, $c_{\text{fight}} = 0.8$, $c_{\text{flee}} = 0.3$, $a_{\text{qual}} = 3$, $a_{\text{status}} = 1$, $h = 0.8$, and $b = 0.1$. The default number of high-quality individuals to low-quality individuals was 50 : 50 for each sex.

The stable solution we found was a condition-dependent ESS in which the acceptance probabilities depended on the male's quality. In the results below, the strategy's behavior is encapsulated by the "preference ratio," the probability of accepting a high-quality female divided by that of accepting a low-quality female. This indicates which type of female a male would prefer if given a choice, and how strong this preference would be; as such, it corresponds to the results most commonly reported in mate-choice experiments.

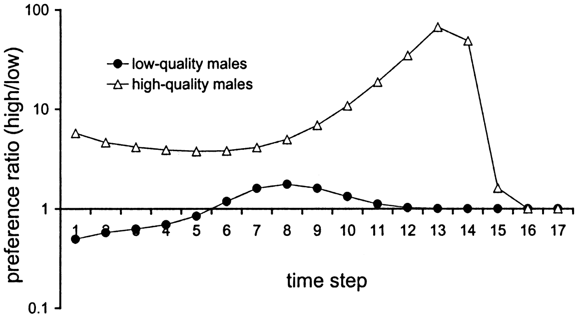
Figure 1 shows the changes in preference of the two types of male over time, for three different frequencies of high-quality females. For both types of male, there is a relative preference for high-quality females for at least some part of the mate-acquisition period, but this preference is much stronger in the high-quality males. As predicted, there are circumstances in which a poor-quality male prefers a poor-quality partner over a high-quality one. This occurs when high-quality females are relatively rare (Figure 1a), and is seen over the early part of the mate-acquisition period. High-quality males never prefer low-quality females. For both types of male, the relative preference for high-quality females is greatest when those females are abundant (Figure 1c). The preference ratio initially increases, but then drops to an equal preference for both types of female in the last few time steps. Low-quality males reach this equal preference earlier than do high-quality males.

Altering the frequency of high-quality males has a qualitatively similar effect, but in the opposite direction. The strongest preferences for high-quality females are seen when there are few high-quality males. Again, there are situations in which low-quality males exert a relative preference for low-quality females in the early part of the mate-acquisition period, i.e., when most of the other males are of high quality.

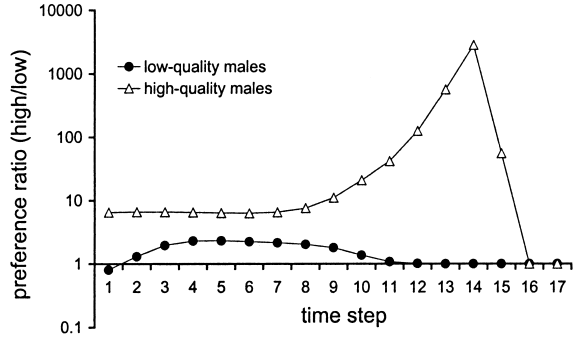
The ratio a_{qual} to a_{status}, reflecting the relative advantage of high-quality males and guarding males in fights, has an important impact on the preference ratios (Figure 2). As the ratio increases, reflecting a reduced advantage to guarding males compared with the advantage to high-quality males, the gradual increase and subsequent drop-off in preference ratio is shifted to later and later time steps. In low-quality males (Figure 2b), it takes place sooner than in high-quality males (Figure 2a), and if the $a_{\text{qual}}/a_{\text{status}}$ ratio is high enough, they even prefer low-quality females to high-quality females at the start of the mate-acquisition period.

High c_{fight} values markedly suppress the increase in preference ratio over time shown by low-quality males (Figure 3b), but have much less effect on the high-quality males (Figure 3a),

(a) 30% high-quality females



(b) 50% high-quality females



(c) 70% high-quality females

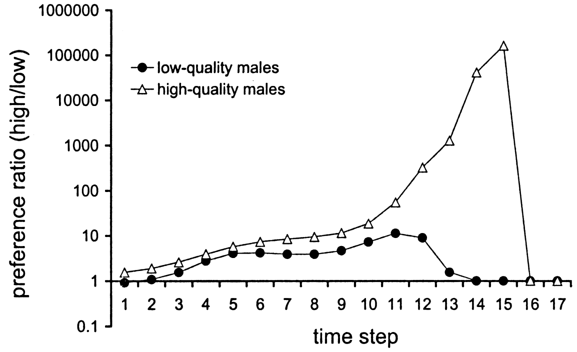
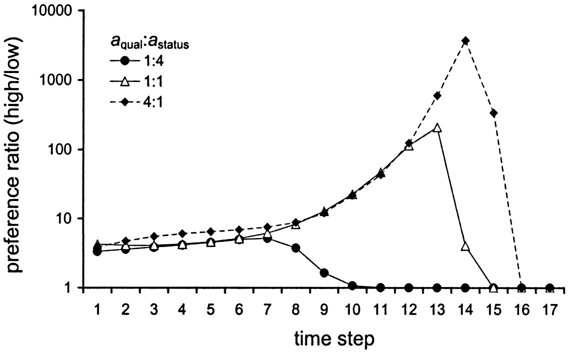


Figure 1
Ratio of preferences for high-quality over low-quality females, as expressed by males of high and low quality over time, in relation to the proportion of females that are of high quality.

(a) high-quality males



(b) low-quality males

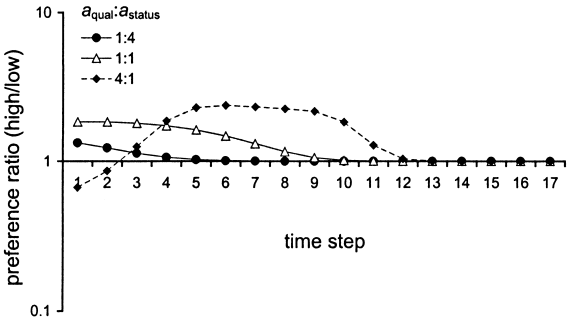


Figure 2
Effect of fighting advantages a_{qual} and a_{status} on the ratio of preferences for high-quality over low-quality females, as expressed by males of high and low quality over time. a_{qual} is the fighting advantage to a high-quality male; a_{status} is the fighting advantage to a guarding male.

who still show huge increases in preference ratio. Curiously, early on in the mate-acquisition period, both types of male show a weaker preference for high-quality females when c_{fight} is small, with low-quality males even preferring low-quality females. At later time steps, this trend is reversed, with males having higher preference ratios at lower c_{fight} values.

Unsurprisingly, these differences between the strategies of low-quality and high-quality males result in assortative mating, with 85% of high-quality males and 68% of low-quality males ending up with a partner of the same quality at the mating point. Increasing the error parameter *b*, so that mistakes are more common, reduces the extent of this assortative mating.

DISCUSSION

Our ESS model predicts several features of mate-choice behavior, some of which are shared by all males and some of which differ between males of high and low quality. We discuss first the features common to all males, then move on to consider quality-dependent differences.

General mate-choice behavior

Under most circumstances, both types of male show a preference for high-quality females over low-quality females. This preference is strongest when high-quality females are common and high-quality males are rare: males are more choosy about their partners when there is a greater chance of finding one of high quality and when the competition for those mates is less fierce. There is empirical evidence that individuals become more choosy if their previous experience suggests that attractive mates are abundant, and, conversely, that they become less choosy if attractive mates appear to be rare. Prior exposure to males with attractive phenotypes has been found to increase the preference for those mates, whereas prior exposure to unattractive males reduces this preference (Bakker and Milinski, 1991; Collins, 1995; Downhower and Lank, 1994; Wagner et al., 2001).

Preference for high-quality mates rises gradually for most of the mate-acquisition period, as the chances of being able to retain a mate till the end increase. This contrasts with the results of an earlier model by Johnstone (1997), who found that only low-quality individuals show increased choosiness over the early part of the mate-acquisition period. The reason for this difference is that in Johnstone's model, individuals leave the breeding pool on finding a desirable mate, whereas in the current model, a paired male can be displaced from his partner by a competitor. Therefore, he runs a high risk of losing a desirable female if he acquires her early on.

As the mate-acquisition period draws to a close, however, choosiness declines. In the last few time steps, all males show a reduced preference for the best females and they become indifferent to the quality of available mates, because there is an increasing likelihood that they will end up without a mate at all. This effect of a finite time horizon has been predicted by earlier models (Johnstone, 1997; Real, 1990) and demonstrated in several empirical studies (see Backwell and Passmore, 1996; Bakker and Milinski, 1991; Thomas et al., 1998).

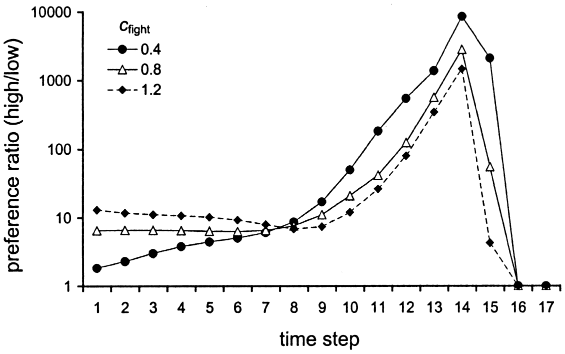
As the fighting advantage to guarding males decreases relative to that to high-quality males, the increase in preference for high-quality females occurs later and later. With lower a_{status}, males cannot expect to be able to hold on to their partner for as long, and so high-quality females become a more attractive option later on. The preference ratio is also affected by the cost of losing a fight, because this affects the frequency of fights and therefore the chances of successfully defending a female acquired early on. The biggest rise in preference for high-quality females over time occurs at low c_{fight} values, at which fights are most common. At early time steps, the preference ratio increases with c_{fight}, such that the strongest relative preference for high-quality females is seen when c_{fight} is high. At these c_{fight} values, guarding males are less likely to be challenged; hence, there is a greater chance of holding on to a high-quality female acquired early on than there would be at low c_{fight} values.

Condition-dependent mate preferences

The results of our model show clear differences between low-quality and high-quality males, both in the strength (choosiness) and direction (preference function) of their preferences. High-quality males are considerably more choosy, showing a preference for high-quality females that is always at least as great as that shown by low-quality males, and that often exceeds it by several orders of magnitude. Furthermore, there are situations when low-quality males also have a different preference function, preferring low-quality females over high-quality females. Such condition-dependence in preference is seen early on and is promoted by intense competition, when high-quality females are rare or high-quality males are common. At the beginning of the mate-acquisition period, it is unwise for a poor-quality male to favor a high-quality female—he is unlikely to be able to fend off other males till the mating point, particularly when the best females are such a highly contested resource.

The preferences of the two types of male differ in several other, more subtle, respects. Low-quality males become indifferent to female quality earlier than do high-quality males; because of their inferior competitive ability, the danger that they will end up without a mate is greater than for their high-quality counterparts. The cost of losing fights also affects their preferences more severely, with high c_{fight} values markedly reducing their preference for high-quality females and containing it to the first half of the mate-acquisition period. Finally, large fighting advantages to high-quality males (high $a_{\text{qual}}/a_{\text{status}}$) can affect low-quality males to such an extent that they may exert a relative preference for low-quality partners early on in the mate-acquisition period.

(a) high-quality males



(b) low-quality males

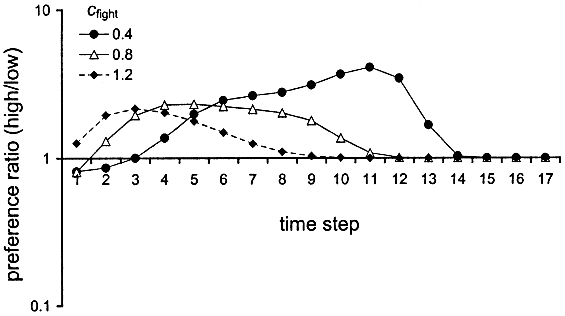


Figure 3
Effect of c_{fight} on the ratio of preferences for high-quality over low-quality females, as expressed by males of high and low quality over time.

The greater competitive ability of high-quality males leads to assortative mating with respect to quality. This is reinforced by the differences in choosiness and preference function between high-quality and low-quality males. Assortative mating by traits indicating quality has been documented in several bird species (Filliater and Breitwisch, 1997; Regosin and Pruett-Jones, 2001; Rintamäki et al., 1998; Roulin, 1999; Roulin et al., 2001) and has been predicted by other models (Johnstone, 1997; Johnstone et al., 1996; Parker, 1983).

Assumptions of the model

To simplify our calculations, we modeled individual quality as a discrete variable with only two possible values. If we were to relax this constraint and allow continuous variation in quality, it is likely that we would obtain similar results. The males of higher quality should still be more likely to obtain higher-quality mates by virtue of their superior competitive ability, and lower-quality males should still prefer lower-quality partners under circumstances of intense competition. Males of intermediate quality should be able to cope with intermediate costs of competition and are most likely to end up with intermediate-quality mates. Thus, assortative mating should emerge along a continuum of male and female quality.

We made the additional simplifying assumption that a male could only obtain one mate; our simulated population was monogamous. If we altered this to model a polygynous system, it would most likely intensify the competition. In the extreme case of a species in which the best-quality males defend large harems of females and the majority of males fail to find a mate, low-quality males should show even less discrimination and have high acceptance probabilities for females of all qualities.

A more complicated model would be needed to examine whether, given this reduced choosiness, low-quality males would prefer the less sought-after, low-quality females to the same extent as in the current model.

The females in our model were entirely passive and unable to reject mates. Again, we made this assumption to simplify our calculations. If we were to extend the model and allow females as well as males to be choosy, we might expect that an already-paired female who was allocated a high-quality male would be more likely to abandon her current partner if he was of low quality rather than high quality. This should reinforce assortative mating and further reduce the preferences of low-quality males for high-quality females.

We have focused in this article on males competing for females, but there is no reason why the consequences of costly competition should be any different for females choosing males. It is likely that in many species, both sexes engage in competition over access to the best mates, and that some individuals are better able than others to withstand the costs this entails. Condition-dependent preferences will emerge in both sexes as a result and presumably will combine to make mating even more strongly assortative.

Studies of mate choice have typically overlooked variation in mate preferences, instead concentrating on the average preference expressed by a group of individuals (for notable exceptions, see Brooks and Endler, 2001; Jennions et al., 1995; Kodric-Brown and Nicoletto, 2001; Møller, 1994; Rowland et al., 1995). Investigating these "population" preferences is a valuable and worthwhile pursuit because it can identify the direction and intensity of sexual selection acting on particular traits, but it is also important to try and understand why individual differences in preference might exist. The findings of our model suggest one reason for this: when competition for mates is costly, we should expect mate preferences to differ simply on the basis of differences in competitive ability. However, variation in mate preferences may occur for a number of other reasons (for review, see Jennions and Petrie, 1997). More empirical and theoretical studies are needed to investigate how and why such variation might be adaptive, and what consequences this might have for processes of sexual selection.

APPENDIX A

Calculating the expected frequencies resulting from the current population strategy

At the start of time step t, the expected frequency of males, F_m, in a certain situation can be written as $F_m(t,q_m,q_f)$, where q_m and q_f are as described in the main text, and q_f takes a value of 0 if the male is unpaired. Similarly, the frequency of females, F_f, in a certain situation at the start of time-step t is written as $F_f(t,q_f,q_m)$, with $1 \leq q_f \leq 2$ and $0 \leq q_m \leq 2$. At the decision point, the frequency of males can be written as $F_{m,dec}(t,q_m,q_f,q_r,s)$, where $0 \leq q_r \leq 2$. For the purposes of calculating optimal male strategies, we can ignore the decision-point frequencies for females.

Given the initial frequencies of unpaired males of high and low quality at the start of time step 1, we can calculate the decision-point frequencies in the same time step according to the equation

$$F_{m,dec}(1, q_m, q_f, 0, 0) = F_m(1, q_m, 0) \times F_f(1, q_f, 0). \tag{A1}$$

From this point we can work out the frequencies of males in different situations in the following time step. Those that are unpaired at the start of $t = 2$ are the ones that rejected the female they were allocated in time step 1:

$$F_m(2, q_m, 0) = \sum_{q_f=1}^{2} F_{m,dec}(1, q_m, q_f, 0, 0) \times (1 - p(1, q_m, q_f, 0, 0)). \tag{A2}$$

Here, $p(1,q_m,q_f,0,0)$ is the probability that the male accepts the female he was allocated, as specified by the population strategy. Some of the males will have rejected low-quality females and others will have rejected high-quality females; hence, we sum the expressions for each female quality. Conversely, males that are paired at the start of $t = 2$ must have accepted the female they were allocated:

$$F_m(2, q_m, q_f) = F_{m,dec}(1, q_m, q_f, 0, 0) \times p(1, q_m, q_f, 0, 0). \tag{A3}$$

The female frequencies at the same point can be calculated simply from the male frequencies, because for any combination of q_m and q_f, $F_f(2,q_f,q_m) = F_m(2,q_m,q_f)$.

We used the same two-stage procedure to find the expected frequencies in later time steps, but our calculations were complicated by the possibility of a rival male being present. The expected frequency of males just allocated to a female at the decision point in time step t is given by

$$F_{m,dec}(t, q_m, q_f, q_r, 0) = F_{m,}(t, q_m, 0) \times F_f(t, q_f, q_r). \tag{A4}$$

For males who are already resident at the decision point, the expected frequencies are

$$F_{m,dec}(t, q_m, q_f, q_r > 0, 1) = F_{m,}(t, q_m, q_f) \times F_m(t, q_r, 0). \tag{A5}$$

for those allocated a rival and

$$F_{m,dec}(t, q_m, q_f, 0, 1) = F_m(t, q_m, q_f) \times \left(1 - \sum_{q_r=1}^{2} F_m(t, q_r, 0)\right) \tag{A6}$$

for those not.

Working out the expected frequencies of different male-female combinations at the start of the next time step is less straightforward, as they are affected by the outcome of fights. Males unpaired at the start of time step $t + 1$ include those who were unpaired at the start of time step t and rejected the female they were allocated; those who were paired at the start of t, were not allocated a rival male but decided to reject their female partner; and males who were paired at the start of t, were allocated a rival, and were either chased off by the challenger or lost a fight to him. Grouping these males together, their frequency is

$$\begin{aligned} F_m(t+1, q_m, 0) &= \sum_{q_f=1}^{2} \sum_{q_r=0}^{2} F_{m,dec}(t, q_m, q_f, q_r, 0) \times (1 - p(t, q_m, q_f, q_r, 0)) \\ &\quad + \sum_{q_f=1}^{2} F_{m,dec}(t, q_m, q_f, 0, 1) \times (1 - p(t, q_m, q_f, 0, 1)) \\ &\quad + \sum_{q_f=1}^{2} \sum_{q_r=1}^{2} F_{m,dec}(t, q_m, q_f, q_r, 1) \\ &\quad \times \begin{pmatrix} (1 - p(t, q_m, q_f, q_r, 1)) \times p(t, q_r, q_f, q_m, 0) \\ + p(t, q_m, q_f, q_r, 1) \times p(t, q_r, q_f, q_m, 0) \times v(q_r, q_m) \end{pmatrix} \end{aligned} \tag{A7}$$

where $v(q_r,q_m)$ is the probability that the rival male wins the fight (see main text).

For males paired to a female of q_f at the start of time step $t+1$, we have to consider: those who were allocated to an unpaired q_f female in time step t and accepted her; those who were already paired to a q_f female at the start of t, were not allocated a rival, and decided to stay with their partner; and those who were already paired to a q_f female at the start of t, were allocated a rival, and either defeated him in a fight or were not challenged. The total frequency of these males is therefore

$$\begin{aligned}&F_m(t+1,q_m,q_f>0)\\ &\quad= F_{m,dec}(t,q_m,q_f,0,0)\times p(t,q_m,q_f,0,0)\\ &\qquad+F_{m,dec}(t,q_m,q_f,0,1)\times p(t,q_m,q_f,0,1)\\ &\qquad+\sum_{q_r=1}^{2}F_{m,dec}(t,q_m,q_f,q_r,1)\\ &\qquad\times\left(\begin{array}{l} p(t,q_m,q_f,q_r,1)\times\left(\begin{array}{l}p(t,q_r,q_f,q_m,0)\times v(q_m,q_r)\\ +(1-p(t,q_r,q_f,q_m,0))\end{array}\right)\\ +(1-p(t,q_m,q_f,q_r,1))\times(1-p(t,q_r,q_f,q_m,0))\end{array}\right)\end{aligned} \tag{A8}$$

where $v(q_m,q_r)$ is the probability that the focal male wins the fight.

Once we have the expected frequencies of males in all possible situations at the start of each time step, it is simple to calculate the corresponding female frequencies. The expected frequency of q_f females paired to a q_m male at the start of time step t is given by

$$F_f(t,q_f,q_m>0)=F_m(t,q_m,q_f) \tag{A9}$$

The expected frequency of q_f females that are unpaired will be equal to the total frequency of q_f females minus the frequencies of those paired to males of all qualities, i.e.,

$$F_f(t,q_f,0)=\sum_{q_m=0}^{2}F_f(1,q_f,q_m)-\sum_{q_m=1}^{2}F_f(t,q_f,q_m). \tag{A10}$$

Because all individuals are unpaired at the start of $t=1$, $\sum F_f(1,q_f,q_m)=F_f(1,q_f,0)$.

Equations A1–A10 allow us to calculate the expected frequencies of males and females of high and low quality in all possible situations at every time step. In the context of these frequencies, we can then compute the expected pay-off to an alternative mutant strategy arising in the population (Appendix B).

APPENDIX B

Calculating the best-response strategy

The end pay-off function, as given in the main text, is

$$W_{\text{start}}(T,q_f)=(q_f/2)\times k \tag{B1}$$

where W_{start} is the male's fitness at the start of the time step, q_f is the female's quality, and k is a constant controlling the difference in pay-off for being paired to a high-quality versus a low-quality female.

Working back from here, we can consider a male in a certain situation at the decision point in the previous time step ($T-1$) and calculate his expected fitness from making each of the two decisions available to him (either accepting the female or rejecting her). For situations in which there is no rival male, this is simply

$$W_{\text{accept}}(T-1,q_m,q_f,0,s)=W_{\text{start}}(T,q_f) \tag{B2}$$

$$W_{\text{reject}}(T-1,q_m,q_f,0,s)=W_{\text{start}}(T,0)=0, \tag{B3}$$

where W_{accept} is the expected pay-off associated with accepting the current female, and W_{reject} is that associated with rejecting her. With a rival male, it becomes more complicated, as we have to also consider the possible outcomes of the conflict:

$$\begin{aligned}&W_{\text{accept}}(T-1,q_m,q_f,q_r,s)\\ &\quad=p(T-1,q_r,q_f,q_m,1-s)\\ &\qquad\times\left(\begin{array}{l}v(q_m,q_r)\times W_{\text{start}}(T,q_f)\\ +v(q_r,q_m)\times(W_{\text{start}}(T,0)-c_{\text{fight}})\end{array}\right)\\ &\qquad+(1-p(T-1,q_r,q_f,q_m,1-s))\times W_{\text{start}}(T,q_f)\end{aligned} \tag{B4}$$

$$\begin{aligned}&W_{\text{reject}}(T-1,q_m,q_f,q_r,s)\\ &\quad=p(T-1,q_r,q_f,q_m,1-s)\times(W_{\text{start}}(T,0)-c_{\text{flee}})\\ &\qquad+(1-p(T-1,q_r,q_f,q_m,1-s))\times W_{\text{start}}(T,q_f).\end{aligned} \tag{B5}$$

The probability the rival male fights, $p(T-1,q_r,q_f,q_m,1-s)$, is defined by the current population strategy. If both males decide they want the female, the outcome of the fight is decided according to Equation 2 in the main text.

Whether or not a rival male is present, we can collect together W_{accept} and W_{reject} to give W_{dec}, the fitness of a male in a certain situation at the decision point. For the decision point in time step $T-1$, this is

$$\begin{aligned}&W_{\text{dec}}(T-1,q_m,q_f,q_r,s)\\ &\quad=p'(T-1,q_m,q_f,q_r,s)\times W_{\text{accept}}(T-1,q_m,q_f,q_r,s)\\ &\qquad+(1-p'(T-1,q_m,q_f,q_r,s))\times W_{\text{reject}}(T-1,q_m,q_f,q_r,s)\end{aligned} \tag{B6}$$

where p' represents the acceptance probabilities of the strategy with the fitness that we are calculating, as distinct from the probabilities, p, of the population strategy it is playing against.

Now, working back a step further, we can use W_{dec} to calculate W_{start}, the expected fitness at the start of that time step. This depends on t, q_m, and q_f, but not on q_r or s because there is no rival present. For unpaired males,

$$\begin{aligned}&W_{\text{start}}(T-1,q_m,0)\\ &\quad=\sum_{q_f=1}^{2}\sum_{q_r=0}^{2}F_f(T-1,q_f,q_r)\times W_{\text{dec}}(T-1,q_m,q_f,q_r,0).\end{aligned} \tag{B7}$$

This sums together all of the decision-point fitness values, W_{dec}, each multiplied by the chance of the male finding himself in that particular situation at the decision point. For paired males,

$$\begin{aligned}&W_{\text{start}}(T-1,q_m,q_f)\\ &\quad=\left(1-\sum_{q_r=1}^{2}F_m(T-1,q_r,0)\right)\times W_{\text{dec}}(T-1,q_m,q_f,0,1)\\ &\qquad+\sum_{q_r=1}^{2}F_m(T-1,q_r,0)\times W_{\text{dec}}(T-1,q_m,q_f,q_r,1).\end{aligned} \tag{B8}$$

The two summed terms in this equation correspond, respectively, to not being allocated and being allocated a rival male.

We are now at the start of the previous time step and can repeat the process to find the expected fitness of males in different situations at the start of time step $T-2$. More generally, we can write the important fitness equations as follows:

$$W_{\text{start}}(t, q_m, 0) = \sum_{q_f=1}^{2} \sum_{q_r=0}^{2} F_f(t, q_f, q_r) \times W_{\text{dec}}(t, q_m, q_f, q_r, 0) \tag{B9}$$

$$W_{\text{start}}(t, q_m, q_f > 0) = \left(1 - \sum_{q_r=1}^{2} F_m(t, q_r, 0)\right) \times W_{\text{dec}}(t, q_m, q_f, 0, 1) + \sum_{q_r=1}^{2} F_m(t, q_r, 0) \times W_{\text{dec}}(t, q_m, q_f, q_r, 1) \tag{B10}$$

$$W_{\text{dec}}(t, q_m, q_f, q_r, s) = p'(t, q_m, q_f, q_r, s) \times W_{\text{accept}}(t, q_m, q_f, q_r, s) + (1 - p'(t, q_m, q_f, q_r, s)) \times W_{\text{reject}}(t, q_m, q_f, q_r, s) \tag{B11}$$

$$W_{\text{accept}}(t, q_m, q_f, 0, s) = W_{\text{start}}(t+1, q_m, q_f) \tag{B12}$$

$$W_{\text{accept}}(t, q_m, q_f, 0, s) = W_{\text{start}}(t+1, q_m, 0) \tag{B13}$$

$$W_{\text{accept}}(t, q_m, q_f, q_r > 0, s) = p(t, q_r, q_f, q_m, 1-s) \times \begin{pmatrix} v(q_m, q_r) \times W_{\text{start}}(t+1, q_m, q_f) \\ + v(q_r, q_m) \times (W_{\text{start}}(t+1, q_m, 0) - c_{\text{fight}}) \end{pmatrix} + (1 - p(t, q_r, q_f, q_m, 1-s)) \times W_{\text{start}}(t+1, q_m, q_f) \tag{B14}$$

$$W_{\text{reject}}(t, q_m, q_f, q_r > 0, s) = p(t, q_r, q_f, q_m, 1-s) \times (W_{\text{start}}(t+1, q_m, 0) - c_{\text{flee}}) + (1 - p(t, q_r, q_f, q_m, 1-s)) \times W_{\text{start}}(t+1, q_m, q_f). \tag{B15}$$

For each possible situation, the best-response strategy should choose with a probability of one whichever option, accept or reject, yields the biggest expected pay-off (i.e., W_{accept} if $W_{\text{accept}} > W_{\text{reject}}$, and W_{reject} if $W_{\text{accept}} < W_{\text{reject}}$). We adjusted the acceptance probabilities of this best-response strategy to account for errors in decision making (see main text).

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