Make Love Not War: When Should Less Competitive Males Choose Low-Quality but Defendable Females?

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Abstract: Male choosiness for mates is an underexplored mechanism of sexual selection. A few theoretical studies suggest that males may exhibit—but only under rare circumstances—a reversed male mate choice (RMMC; i.e., highly competitive males focus on the most fecund females, while the low-quality males exclusively pair with less fecund mates to avoid being outcompeted by stronger rivals). Here we propose a new model to explore RMMC by relaxing some of the restrictive assumptions of the previous models and by considering an extended range of factors known to alter the strength of sexual selection (males' investment in reproduction, difference of quality between females, operational sex ratio). Unexpectedly, we found that males exhibited a reversed mate choice under a wide range of circumstances. RMMC mostly occurs when the female encounter rate is high and males devote much of their time to breeding. This condition-dependent strategy occurs even if there is no risk of injury during the male-male contest or when the difference in quality between females is small. RMMC should thus be a widespread yet underestimated component of sexual selection and should largely contribute to the assortative pairing patterns observed in numerous taxa.

Keywords: sexual selection, male mate choice, intrasexual competition, competitive ability, assortative pairing, dynamic game.

Introduction

In classical sexual-selection theory, it is mainly males that are considered to be the sex that competes for access to mates because their potential reproductive rate is higher than that of females (which are therefore expected to be the choosy sex; Trivers 1972; Parker 1983; Clutton-Brock and Vincent 1991; Andersson 1994). In contrast to this dichotomous view, evidence of male choosiness is accumulating (Amundsen and Forsgren 2001, 2003; for reviews, see Bonduriansky 2001; Clutton-Brock 2007; Kokko and Jennions 2008) for species with conventional sex roles (i.e., species where the operational sex ratio—the ratio of ready-to-mate males to ready-to-mate females—is male biased). This has triggered a renewed interest in theoretical investigations of male or mutual mate choice (Rowell and Servedio 2009; see table 1).

Males have recently been shown to differ in their choosiness for mates according to their own quality (in humans: Pawlowski and Dunbar 1999; Buston and Emlen 2003) and relative competitive ability (in spiders: Bel-Venner et al. 2008; in fish: Candolin and Salesto 2009). These studies suggest that assortative mating, a pattern that is widely observed in numerous taxa (Crespi 1989; Shine et al. 2001; Hoefler 2007; Pryke and Griffith 2007), may be partly mediated by differential male mate choice and fueled by internmale competition. In support of this, two recent empirical studies have shown that mating preferences of males vary with their competitive ability and mating preference for low-quality females occurs in the field (Bel-Venner et al. 2008) and the laboratory (Candolin and Salesto 2009). When competition between males is strong, the most competitive males (i.e., the larger ones [Bel-Venner and Venner 2006] or those in better condition [Candolin and Salesto 2009]) primarily pair with the most fecund females, while smaller males focus on less fecund females (Bel-Venner and Venner 2006) or become indiscriminate (Candolin and Salesto 2009), which results in size-assortative pairing. Because such studies are rare, it is unclear whether these results reflect a general yet so far largely unexplored pattern of sexual selection. Theoretical investigation is required to explore the general conditions under which condition-dependent mate choice strategies emerge in males on the basis of their competitive ability.

Most theoretical studies exploring mate choice (table 1) have assumed that males are either unselective or, if they are choosy, always prefer high-quality females. However, Fawcett and Johnstone (2003) and then Hardling and Kokko (2005) pointed out that such a pattern of selectivity would mean that the level of male-male competition should vary with the quality of females in the population,
Male Mate Choice and Assortative Pairing

Table 1: Overview of the parameters tested in models of mutual or male mate choice

<table>
<thead>
<tr>
<th>Model, source</th>
<th>Male competitive ability</th>
<th>Cost of fight</th>
<th>Proportion of high-quality males</th>
<th>Proportion of strong competitors</th>
<th>Mate density</th>
<th>Mate quality</th>
<th>Reproductive investment</th>
<th>Mortality during breeding/searching</th>
<th>OSR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mutual mate choice:</td>
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<tr>
<td>Johnstone et al. 1996</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
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<tr>
<td>Johnstone 1997</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td>Kokko and Monaghan 2001</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Kokko and Johnstone 2002</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Servedio and Lande 2006</td>
<td>X</td>
<td>X</td>
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<td>Male mate choice:</td>
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<tr>
<td>Fawcett and Johnstone 2003</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td>Harälding et al. 2004</td>
<td>X</td>
<td>X</td>
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<tr>
<td>Harälding and Kokko 2005</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td>This study</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
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</tr>
</tbody>
</table>

Note: OSR = operational sex ratio, the ratio of ready-to-mate males to ready-to-mate females.

as competition should be more intense for the highest-quality (e.g., the most fecund) females. Such heterogeneity in competition could favor mating preferences among males according to their own competitive ability. Indeed, low-quality males could trade quality for security; by actively avoiding the highest-quality females and focusing on the low-quality ones, they would reduce competition with their stronger competitors and thus increase their chances of mating successfully (Fawcett and Johnstone 2003; Härälding and Kokko 2005).

In their pioneering study, Fawcett and Johnstone (2003) suggested that weakly competitive males might preferentially pair with low-quality females; yet, in their model, the reversed male mate choice pattern (RMMC; i.e., when good competitors avoid low-quality females while weak competitors simultaneously avoid high-quality females and focus on low-quality ones) was found only under rare circumstances, especially when high-quality females were scarce relative to low-quality ones. In their study, it was also assumed that a male would mate with a single partner during his lifetime, which would be likely to strongly affect his selectivity and mating preferences. Härälding and Kokko (2005) integrated multiple mating into their model and found that RMMC is a more common outcome, with “prudent” low-competitive males avoiding high-quality females. For simplicity, however, Härälding and Kokko (2005) made several restrictive assumptions that are likely to increase the occurrence of an RMMC. In particular, they assumed that only large males can take over females, and only from small males. Consequently, among paired males, only weak competitors can be challenged, and hence, weak males benefit disproportionately from reduced competition if they focus on low-quality, less attractive females. Thus, the conditions to which these models apply are relatively limited, and it is not possible to infer whether condition-dependent male mate choice strategies might be widespread. Notably, neither the reproductive investment of males, the operational sex ratio, nor the quality differences between females have been explored for effects on male choice, despite their major impact on sexual-selection processes (see table 1; Trivers 1972; Parker 1983; Owens and Thompson 1994; Kvarnemo and Ahnesjo 1996; Parker and Simmons 1996; Kvarnemo and Simmons 1999; Kokko and Jennions 2008). Similarly, a related set of models on mutual mate choice outlines conditions under which both male and female choosiness are expected as a function of these factors, but it does not consider the differential male competitive ability that might have a major impact on the observed mating patterns (first five rows of table 1).

To clarify the foregoing issues, we provide a model that explores the conditions under which males switch from pairing opportunistically to pairing exclusively with females of a given quality. We consider a wider range of parameters than any previous examination of male choice, including factors known to alter the strength of sexual selection and affect the payoff for defending a female of a given value (table 1). We use our results to make inferences about the types of systems in which condition-dependent male mate choice may be common and may underlie assortative mating patterns.

Our model is based on precopulatory mate guarding by males. For simplicity, we assume throughout this study that females’ decisions are negligible in the pairing process, provided that females’ selectivity for mates is likely to reinforce the patterns of assortative pairing (Johnstone 1997). Given the results of previous theoretical studies on mutual mate choice (see table 1), we predict in our study that the most competitive males would be increasingly choosy toward high-quality females when (1) the female encounter rate increases (along with mating opportuni-
Figure 1: Dynamics of male activity and pairing status. A. At any time $t$, an unpaired male of quality $q$ may suffer a basic predation risk while roaming ($\beta_b$, which is always set to 0 except in fig. A3 in the online edition of the *American Naturalist*). If he survives, he may encounter an unpaired female of fecundity $f$ with the probability $\lambda_{f,s}$. Depending on his decision ($C_{s,0}$), he may either start guarding her or reject her and remain unpaired at the next time step. Any male must guard his mate for a fixed period, $h_{\text{max}}$, before mating occurs. Alternatively, he may encounter a female $f$ that is already paired with a male $q_{r}$ with the probability $\lambda_{f,q_{r}}$. Depending on his decision, he may reject the female or challenge the resident male; if he wins the fight (with the probability $1-r_{q,r}$), he becomes paired at the next time step; if he loses the fight, he may die (with...
ties), (2) the time investment of a male in each mating event increases (due to the increasing contribution of each mating event to his lifetime reproductive success), (3) differences in female quality become greater (males benefit more from avoiding low-quality females), or (4) the operational sex ratio (OSR) is less male biased (thus reducing competition between males). Unlike classical predictions of sexual-selection theory, however, we expect that condition-dependent mate choice strategies will emerge among males whenever the strongest competitors focus on the highest-quality females: weak males should then reject high-quality females and select lower-quality ones due to their lower attractiveness to competitors. This model allows us to evaluate the sensitivity of the mate choice of males with distinct competitive abilities to the time they must invest per mating event, the female encounter rate, the range of fecundity values among females, and the OSR. To extend the scope of our study, we also investigate the consequences of the risk of injury and death due to fighting and the mortality risk associated with breeding (when males either search for or guard a mate) for male strategies (see the appendix in the online edition of the American Naturalist). We assess the impact of male mate choice on the occurrence of assort ed pairs (i.e., the preferential pairing between mates of the same quality, reflected by the competitive ability of males and the fecundity of females).

Some general conclusions may be drawn from our model. First, it relaxes some restrictive assumptions by allowing (1) males to mate several times sequentially throughout their lives and (2) strong as well as weak competitors to successfully take over a female from a rival male. Second, this model incorporates major predictors of the intensity and direction of sexual selection and explores their influence on males’ selectivity for mates. Notably, time investment per mating accurately reflects the breeding cost (Parker 1974) and, by extension, the parental investment of males (sensu Trivers 1972). Predictions of this model could apply to numerous mating systems, from those with almost no male investment to those with extreme male reproductive effort.

The Model

Because the decision for a male to pair with a female might be closely linked both to his own status (quality [competitive ability], age, and guarding status) and to the strategies adopted by other males in the population, we developed a dynamic game (Houston and McNamara 1999; Clark and Mangel 2000). We consider the optimal pairing strategy of males living throughout their adult lives in a system where a male must guard a female for a fixed period before he can mate with her, fertilize her eggs, and then leave her. Throughout the guarding period, the resident male can be dislodged by a rival male who will then, in turn, have to guard the female for the fixed period before receiving fitness returns. In our model, only pairs can be formed; that is, each female can be guarded by at most a single male, and a male cannot guard several females simultaneously. Because the longevity of an adult male is at least twice as long as the time he must invest in one mating event, a male may potentially mate with two or more partners during his lifetime.

The model predicts how selective an unpaired male must be whenever he encounters a potential mate and his choosiness as a function of his own competitive ability (low or high), the female’s quality (low or high fecundity), and her pairing status (unpaired or already paired with a male of either high or low competitive ability).

The Dynamic State–Dependent Model

The modeled period corresponds to the longevity of an adult male and is divided into a series of discrete time steps \((t = 0, 1, \ldots, T - 1, T)\). At time \(t = 0\), the male reaches sexual maturity, and at the time horizon \((T)\) he is no longer sexually active. We divide time in small enough units \((T = 10,000)\) to ensure that, within a time step, a roaming male cannot encounter more than one female and a female cannot be visited by more than one male.

We consider that the state of a female in the population is defined by her quality \((f)\) and her pairing status \((s)\).
Quality \( q \) is fixed for a female, and it reflects either low \((q = 1)\) or high \((q = 2)\) fecundity. When mating with a female, a male gains a fitness return \( \omega \) that is proportional to her fecundity \((\omega_q < \omega_g)\). We define three distinct pairing statuses \( s \) for a female: she may be unpaired \((s = 0)\) or guarded by either a low- or a high-quality male \((s = 1\) or 2, respectively).

The state of a male is defined by three distinct components: his quality, \( q \), reflects his competitive ability, and this value remains constant throughout his life (he can be either a poor \([q = 1]\) or a good \([q = 2]\) competitor); his pairing status, \( g \), may fluctuate over time \((g = 0, 1, \text{or } 2)\), for a male that is unpaired or paired with either a low- or a high-quality female, respectively), and \( h \) is the number of time steps that remain before a paired male can copulate with his mate. A value of \( h = -1 \) is attained when a male is unpaired.

The dynamics of a male’s activity and pairing status is detailed in figure 1. When unpaired (fig. 1A), a male is searching for a mate. At any time while guarding, a paired (resident) male can be challenged by an intruder; if the resident male is dislodged, he does not get any fitness rewards from that mate (fig. 1B). The probability that a resident male will successfully resist a takeover attempt depends on both his own competitive ability and that of his challenger (see “Probability of a Resident Male Resisting a Takeover Attempt and the Risk of Dying during Conflict” in the appendix in the online edition of the American Naturalist).

Any action of a male searching for a mate is defined by a dual guarding criterion \((a_p, a_g)\): one criterion for low-quality females \((a_p)\) and one for high-quality females \((a_g)\). For each female quality, we define four selectivity thresholds, from \(-1\) to 2, along a decreasing gradient of choosiness (see table A1 in the online edition of the American Naturalist). When encountering a female of fecundity \( f \), if \( a_p = -1 \), then the male will reject her, whatever her pairing status. Notably, our system allows males to focus on females of a given quality while completely ignoring other females. If \( a_p = 0 \), a male is willing to guard a female of fecundity \( f \) but only if she is unpaired. For \( a_p = 1 \), he is willing to guard her if she is unpaired or, if she is already being guarded, he will challenge only low-quality resident males. For \( a_p = 2 \), he is willing to guard her whatever her pairing status. This classification implies that any male willing to fight with a good competitor \((a_p = 2)\) is also willing to fight with a poor one.

A male looking for a mate has to choose between 16 actions corresponding to all possible combinations of the four guarding criteria for each of the two female qualities. The action chosen at time \( t \) determines the male’s decision if he encounters any female of fecundity \( f \) and pairing status \( s \) (i.e., whether he is willing to guard her). We used a backward procedure to compute the fitness \( W_{a_p,a_g}(q, g = 0, h = -1, t) \) of a single male of quality \( q \) with the dual criterion \((a_p, a_g)\), searching for a mate at time \( t \) (eq. [A2] in the online edition of the American Naturalist). The optimal dual guarding criterion \( A^* = (a_p^*, a_g^*) \) maximizes the fitness equation \( W_{a_p,a_g}^* \):

\[
W_{a_p,a_g}^*(q, g = 0, h = -1, t) = \max_{a_p,a_g} W_{a_p,a_g}(q, g = 0, h = -1, t).
\]  

(1)

The fitness equation of a guarding male is detailed in the appendix in the online edition of the American Naturalist (“Computing Male Fitness”).

Finding the Evolutionarily Stable Strategy

The density of males and females in the infinite population (defined by the number of males and females, respectively, per surface unit) is constant over time. For each sex, we assume that there is an equal number of low- and high-quality individuals in the population (see table 2). The ratio of male to female density accurately reflects the operational sex ratio (OSR), since all males and females are sexually active. The optimal strategy of a male depends on both the availability of mates in the population—and their distribution between all possible states (fecundity, pairing status)—and the strategy followed by unpaired males in the population. To find the evolutionarily stable strategy (ESS), we use a dynamic game that iterates the best response map through successive backward and forward procedures (McNamara et al. 1997; Houston and McNamara 1999; Clark and Mangel 2000; see “Solving the Evolutionarily Stable Strategy” in the appendix in the online edition of the American Naturalist). To help achieve convergence toward the ESS, we introduced errors in behavioral decisions as well as damping, a technique that reduces variations in population parameters from one iteration to the next (for further details see “Solving the Evolutionarily Stable Strategy” in the appendix). At the end of each iteration, we compute the new, stable distribution in the population of males of quality \( q \) according to pairing status \( g \). From this distribution, we update the two population parameters used in the backward procedure at the next iteration. The first parameter is the probability \( \lambda_s \), that a solitary male will encounter a female of fecundity \( f \) and pairing status \( s \) per time unit, which is computed as follows:

\[
\lambda_{s,f} = \sigma d_{s,f}.
\]  

(2)

This probability is positively related to the density of females of a given fecundity and pairing status \( d_{s,f} \), multiplied...
by the mate-searching efficiency $\sigma$, which is constant throughout the study and is related to both the intrinsic ranging ability of males and their ability to detect females. The second parameter is the challenge rate $\tau_{q,f}$, which is the probability that a male of quality $q$ guarding a female of fecundity $f$ will be visited and challenged by an intruder of quality $q_i$ per time unit (see eqq. [A12]–[A15] in the online edition of the *American Naturalist*).

**Computing the Rejection Index**

In this study, we focus on the conditions under which males reject females of a given quality. Our results thus show the willingness of a male of quality $q$ to reject any female of a given fecundity $f$ that he encounters. To do this, we computed a rejection index (RI) for each combination of male and female qualities (see “Computing the Rejection Index,” in the appendix). This index, ranging from $-1$ to $+1$, is the relative difference between the fitness gain a male can expect from rejecting a female of a given quality and the highest fitness gain among his three other possible decisions (accepting her only if she is unpaired, unless she is guarded by a high-quality male, or in all circumstances, respectively). When RI has a positive value, rejecting the female is the optimal action; conversely, a negative value means that one of the remaining actions—that is, guarding the female at least if she is unpaired—is optimal. The selective value of rejecting or accepting the female is higher when RI gets closer to either $0$, $+1$, or $-1$, respectively. The parameters used are summarized in Table 2, in table A2 in the online edition of the *American Naturalist*, and in the figure legends.

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### Table 2: Parameters of the model

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$q_i$</td>
<td>Quality. Competitive ability of males: $x = r$ if resident, $x = i$ if intruder. Fecundity of females: $x = f$.</td>
<td>1 (low); 2 (high)</td>
</tr>
<tr>
<td>$g$</td>
<td>Pairing status of a male</td>
<td>0 (unpaired); 1 (paired with a low-quality mate); 2 (paired with a high-quality mate)</td>
</tr>
<tr>
<td>$s$</td>
<td>Pairing status of a female</td>
<td>0 (unpaired); 1 (paired with a low-quality mate); 2 (paired with a high-quality mate)</td>
</tr>
<tr>
<td>$h$</td>
<td>Time left before a paired male can mate with his partner</td>
<td>From $h_{min}$ to 0; $h = -1$ for an unpaired male</td>
</tr>
<tr>
<td>$t$</td>
<td>Time unit</td>
<td>From 0 to $T = 10,000$</td>
</tr>
<tr>
<td>$\tau_{q,s}$</td>
<td>Probability for a resident male $q_i$ to resist a takeover attempt by an intruder $q_q$</td>
<td>See equation (A1) in the online edition of the <em>American Naturalist</em></td>
</tr>
<tr>
<td>$c$</td>
<td>Maximum advantage a resident male can have in a fight</td>
<td>$c = .95$, except in figure A2 in the online edition of the <em>American Naturalist</em> (where $c = .5$); see equation (A1)</td>
</tr>
<tr>
<td>$\beta_h$</td>
<td>Breeding mortality risk per time unit for a male</td>
<td>0, except in figure A3 in the online edition of the <em>American Naturalist</em> (.0003)</td>
</tr>
<tr>
<td>$\beta_s$</td>
<td>Mortality risk for a male when losing a conflict</td>
<td>0, except in figure A4 in the online edition of the <em>American Naturalist</em> (.05)</td>
</tr>
<tr>
<td>$\omega_i$</td>
<td>Number of eggs a male fertilizes when mated with a female $q_i$</td>
<td>$\omega_i = 50–1,000$; $\omega_2 = 1,000$</td>
</tr>
</tbody>
</table>

#### Demography:

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$d_q$</td>
<td>Density of males of quality $q$</td>
<td>$d_{q+1} = d_{q+2}$</td>
</tr>
<tr>
<td>$d_f$</td>
<td>Density of females of fecundity $f$</td>
<td>$d_{p+1} = d_{p+2}$</td>
</tr>
<tr>
<td>$(d_{q+1} + d_{p+2})/(d_{q+1} + d_{p+2})$</td>
<td>OSR*</td>
<td>$.2$–$2.5$</td>
</tr>
</tbody>
</table>

#### Parameters related to female encounters:

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_{q,s}$</td>
<td>Probability a male finds a female of quality $f$ and pairing status $s$ per time unit</td>
<td>See equation (2)</td>
</tr>
<tr>
<td>$\sigma$</td>
<td>Intrinsic factor of mate-searching efficiency</td>
<td>Constant (.0001)</td>
</tr>
<tr>
<td>$E$</td>
<td>Female encounters*; $E = T \times \sum_i \lambda_i$, 1–200</td>
<td></td>
</tr>
<tr>
<td>$\tau_{q,f}$</td>
<td>Probability for a given pair $q_f$ to be found and challenged by any intruder $q_i$ per time unit</td>
<td>See equations (A12)–(A15) in the online edition of the <em>American Naturalist</em></td>
</tr>
</tbody>
</table>

* For a given, constant female density, the operational sex ratio (OSR) is modified by changing the male density.

* $E$ is the total number of females a solitary male would encounter, on average, during his life if he survives until time $T$. 

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*See the online edition of the *American Naturalist*.*
**Results**

**Male Selectivity, Female Encounters, and Male Reproductive Investment**

When females are scarce, males pair indiscriminately, irrespective of their competitive ability (fig. 2; when the probability of encountering a female is low, all RI values are close to $-1$). When encountering females becomes more likely (from about 10 females encountered, on average), males become selective. Highly competitive males focus on the most fecund females (fig. 2A) and reject low-quality ones (fig. 2B). The results are more variable for weak competitors and depend on their time investment per mating event: when this investment is low (less than 20% of their adult lifetime; $X$-axis), these males behave like high-quality ones (fig. 2C, 2D). For greater time-investment values (more than 25% of their adult lifetime; $X$-axis), poor competitors benefit from reversing their pairing preferences, focusing on the less fecund females (fig. 2D) and rejecting the most fecund ones (fig. 2C). This stems from the fact that the number of visits made by challengers—and among them, good competitors—to one pair increases along with the time a male must spend near his mate (fig. A1 in the online edition of the *American Naturalist*).

**Figure 2:** Male selectivity as a function of reproductive investment and of the probability of encountering a female. The rejection index (RI; $Z$-axis) illustrates the motivation of a male to reject females of a given quality (see “Computing the Rejection Index” in the appendix in the online edition of the *American Naturalist*). RI is shown as a function of the time investment by a male in each reproductive event ($X$-axis, ranging from 1% to 50% of his sexually active lifetime), and of female encounters ($Y$-axis, ranging from 1 to 200, which is the number of females a male is expected to encounter throughout his adult life if he never guards females; see table 2). $A$ and $B$ show the RI of highly competitive males toward high- and low-quality females, respectively (large and small male and female symbols represent high- and low-quality individuals, respectively); $C$ and $D$ show the RI of weak competitors toward high- and low-quality females, respectively. For all cases, there is no mortality risk, the operational sex ratio (OSR; the ratio of ready-to-mate males to ready-to-mate females) is balanced ($OSR = 1$), and high-quality females are twice as fecund as low-quality ones (1,000 and 500 eggs, respectively).
Male Mate Choice and Assortative Pairing

Figure 3: Male selectivity as a function of the fecundity difference between low- and high-quality females and of the probability of encountering a female. See the legend of figure 2 for the descriptions of the Y- and Z-axes and for descriptions of A–D. The X-axis shows the percentage of fitness returns a male gains by mating with a low-quality female as compared with a high-quality one (1,000 eggs), and it ranges from 5% (large difference between low- and high-quality females) to 100% (no difference). For all cases, there is no mortality risk, the operational sex ratio is balanced (OSR = 1), and males must invest 25% of their sexually active lifetime in each reproductive event.

Naturalist): thus, for a poor competitor guarding a highly fecund female, there is an increased probability for him to lose his mate before obtaining any fitness returns (fig. A1).

We obtain the same pattern of mate selectivity when the two categories of males are closer to each other in competitive ability (fig. A2 in the online edition of the American Naturalist). When we introduce a breeding mortality risk for males (fig. A3 in the online edition of the American Naturalist), the reversed mate choice pattern emerges (i.e., poor competitors avoid the most fecund females while good competitors avoid low-quality ones) for a wider range of parameters and from lower time investment values (from 10% of a male’s adult lifetime), compared with the simple situation with no mortality risk.

We now consider a situation in which males must heavily invest in each mating event (one-fourth of their adult lifetimes; fig. 3). If the fecundity of low-quality females is less than 95% of that of the most fecund ones, good competitors should avoid less fecund females (fig. 3A, 3B). Poor competitors also avoid less fecund females when their own relative fecundity is low (fig. 3D). The reversed mate choice pattern emerges from a medium probability of encountering a female and when female quality converges (fig. 3B, 3C). When both types of females are equally fe-
Male selectivity as a function of the operational sex ratio (OSR) and of the probability of encountering a female. See figure 2 for the descriptions of the Y- and Z-axes and for descriptions of A–D. The X-axis shows the OSR ranging from 0.2 (female biased) to 2.4 (male biased).

For all cases, losing a conflict does not entail any mortality risk, males must invest 25% of their sexually active lifetime in each reproductive event, and high-quality females are twice as fecund as low-quality ones (1,000 and 500 eggs, respectively).

cund, both types of males obviously become opportunistic (fig. 3; RI drops to −1 for a fecundity ratio of 100%).

Male Selectivity, Operational Sex Ratio, and Mortality Risk during the Contest

Mate choice strategies of males strongly vary with the OSR (fig. 4): when the operational sex ratio is female biased (OSR < 1), all males focus on the most fecund females (fig. 4A, 4C) and reject the less fecund ones (fig. 4B, 4D). For a more balanced OSR, the selectivity of highly competitive males remains unchanged, whereas that of weak competitors switches abruptly. These males focus on the less fecund mates (fig. 4D) and start avoiding the most fecund ones (fig. 4C). When the OSR becomes male biased, the challenge rate increases, together with the probability that a paired male will be dislodged before he can get any fitness return from his mate. Highly competitive males start pairing opportunistically and no longer reject less fecund females (fig. 4B, for high values of both OSR and female encounters). Competition then uniformly spreads over all the females in the population, regardless of their quality. In such a context, the expected fitness gain for less competitive males is almost zero, whatever they decide, as shown by the almost null value of their RI toward females of either category. For a given, constant, male-biased OSR value (e.g., OSR = 1.5), good competitors are more willing to pair with a low-quality female when the probability of encountering a female increases (i.e., when the female density increases), because male density necessarily increases along with that of females. When both the male and female densities increase, there is therefore a growing number of males that are expected to challenge a pair throughout one guarding session, the competition between...
males increases, and the probability that a male successfully guards one mate becomes very low. As a result, good competitors start pairing opportunistically.

In all the previous situations, the challenger and the resident male incurred no mortality risk while fighting, so that the only competition-dependent risk for a resident male was that of losing his mate by being displaced by a challenger before he attains any fitness return. Whenever a male that loses a conflict incurs a significant risk of dying, the rejection behavior of less competitive males toward the most fecund females emerges more abruptly and for an extensive range of parameters (fig. A4 in the online edition of the *American Naturalist*).

In all of the situations previously described, the assortment between mates according to their quality was strongest whenever weak competitors accepted low-quality females (see figs. A5–A7 in the online edition of the *American Naturalist*). Whenever males exhibited the reversed mate choice pattern, we observed a strong assortative pairing in the population: given the high pairing rate (∼90% of the females of both qualities were paired), no less than 90% of the pairs were assorted, high-quality males paired with the most fecund females, and weak competitors paired with the least fecund females (see figs. A5–A7).

**Discussion**

Our model was designed to explore the variations of mate choice by males according to their individual competitive ability. We show that the RMMC can be favored under a wider range of circumstances than was previously thought (Fawcett and Johnstone 2003; Hårdling and Kokko 2005). In our model, such a pattern emerges whenever highly competitive males exclusively select the most fecund females and when competition is intense between the males in the population. Under these conditions, the level of competition between males differs markedly, depending on the quality of the females over which they are competing. Because less fecund females are not coveted by highly competitive males, they represent “secure mates.” The weakest competitors benefit from focusing exclusively on these females, as they offer a chance to obtain fitness benefits. More specifically, our results show that the RMMC pattern emerges when males heavily invest in each mating event (fig. 2) and when their chance to encounter a female is medium or high under a balanced operational sex ratio (fig. 4). This pattern would be favored when males incur a significant breeding mortality risk during either searching or guarding a mate (fig. A3). Surprisingly, the RMMC pattern emerges even when males suffer neither injury nor mortality risk while fighting (figs. 2, 3) and when there is little variation in female fecundity (fig. 3).

We show that mate choice can be expected to differ considerably between males, depending on the time investment involved in each guarding event (fig. 2). The probability that a paired male will lose the female before obtaining any fitness return increases with the time he has to spend near his mate, due to the growing number of potential challengers occurring over the course of the guarding period (fig. A1). As a result, when the time investment per guarding event is very low, the probability that a guarding male will be challenged is so small that any male can benefit from selecting only high-quality females. When the delay increases, it still benefits strong competitors to select the most fecund females, which is in agreement with previous models on mutual mate choice that suggest that the selectivity for mates increases along with the reproductive investment (Kokko and Monaghan 2001; Kokko and Johnstone 2002). In this situation, our model predicts that weak competitors gain by switching their mating reference and focusing on less fecund females in order to avoid losing to stronger challengers. When each mating event is costly in terms of time, our results thus suggest that the RMMC pattern should emerge, even when the difference in female quality is very low (fig. 3).

Nevertheless, the reversed mate choice pattern can also arise when males do not invest much time per mating event, notably when males suffer a breeding mortality risk such as predation while roaming or pairing (fig. A3). Because males incurring such mortality experience a reduced life span, any guarding event then represents a large part of their expected lifetime. Hence, this would favor the RMMC pattern in the same way that a situation of high time investment—but without any risk—would. In agreement with the study of Hårdling and Kokko (2005), we also show that the RMMC pattern is reinforced when conflicts are costly, that is, in our model, when the loser of a fight risks high mortality (fig. A4). In this situation, to reduce the mortality risk, poor competitors should primarily avoid fighting, especially against high-quality males, by avoiding the most fecund females.

In our model, assortative pairing emerges largely because weak competitors accept low-fecund females while highly competitive males focus on high-fecundity females (see figs. A5–A7). When poor competitors reverse their choice, a vast majority of females in the population become paired with males who match their relative quality. Assortative mating is therefore expected to be a by-product of condition-dependent male mate choice, and it depends on the intensity of the competition between males. Whenever competition is sufficiently intense (i.e., under a male-biased operational sex ratio; fig. A7), good competitors benefit from maximizing their chance of finding and accepting any mate, even a low-quality one. The poorest competitors then no longer benefit from avoiding the most
fecund females. Consequently, most females are paired with the strongest competitors, and there is no significant assortative pairing.

Future theoretical approaches should focus on the RMMC pattern. Models could be designed to test whether mutual mate choice (Johnstone et al. 1996; Johnstone 1997; Kokko and Monaghan 2001; Kokko and Johnstone 2002) reinforces such reversed strategies of males. For instance, as is suggested in several studies (Parker 1983; Gibson and Langen 1996; Johnstone 1997; Fawcett and Johnstone 2003), high-quality females could exhibit a preference for high-quality males, which would lead the weakest males to select less fecund but also less selective mates. Moreover, a lower competitive ability of small males, which is largely the rule in most animal taxa (Blanckenhorn 2005), might be counterbalanced by their more efficient locomotor activity (Moya-Larano et al. 2002; Venner et al. 2003). This would enable small males to find their mates more quickly than large ones, so that they could benefit from maximizing the number of low-quality mates rather than focusing on high-quality ones. This would thus reinforce size-assortative pairing patterns.

Our theoretical study shows the general conditions under which it benefits males to avoid pairing with high-quality females. We found such mate rejection by weak competitors in numerous situations, suggesting that this could be an underestimated mechanism of sexual selection (Crespi 1989; Shine et al. 2001; Hoeffer 2007; Pryke and Griffith 2007). This mechanism should be widespread, since it requires neither costly conflicts between males nor strong differences in the qualities of mates. The reversed mate choice pattern is expected particularly when (1) males must invest heavily in each reproductive event (e.g., pre- or postcopulatory mate guarding or paternal investment [spiders: Bel-Venner et al. 2008; birds: Pryke and Griffith 2007; humans: Pawlowski and Dunbar 1999; Buston and Emlen 2003]), (2) males incur a significant mortality risk when seeking females (diseases and/or predation; insects: Dunn et al. 2001; crustaceans: Jivoff 1997; fishes: Wong and Jennions 2003), or (3) the risk of injury among fighting males is high (fishes: Schuett 1997; birds: Piper et al. 2000). With that prospect in view, our theoretical work highlights the need for further empirical investigations of variation in male mate choice as a function of competitive ability.

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