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Previous experiences shape adaptive mate preferences

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Existing models of mate choice assume that individuals have perfect knowledge of their own ability to attract a mate and can adjust their preferences accordingly. However, real animals will typically be uncertain of their own attractiveness. A potentially useful source of information on this is the feedback from previous encounters with potential mates. Here, we develop a dynamic model of mutual mate choice in which both males and females are initially ignorant of their own attractiveness. Individuals sequentially sample potential mates and retain some information about the outcome of these encounters (e.g., the number of times they are accepted or rejected). We use a simplified process of mutation and selection to evolve an adaptive strategy for mate choice under these conditions. The stable strategy we find is the one in which individuals are sensitive to this previous experience, adjusting their mate preferences according to the interest received from members of the opposite sex. In general, experiences of rejection tend to reduce choosiness, whereas experiences of acceptance tend to increase it. Sensitivity to previous experiences allows individuals to exercise a prudent mate-choice strategy in which their preferences are gradually tuned to their prospects on the mating market. This flexibility is based on simple rules and does not require sophisticated cognitive abilities. Our basic predictions can be tested in systems where both males and females are choosy, and it is possible to manipulate the level of interest shown by potential mates. *Key words:* condition-dependent choice, dynamic game, learning, mutual mate choice, search rules. *[Behav Ecol 20:68–78 (2009)]*

Studies of mate choice in a large array of species have documented which traits individuals prefer in a mate and in some cases have hinted at the benefits they gain from doing so (for a review, see Andersson 1994). This suggests a rather simple view of sexual selection in which all individuals strive to obtain a highly attractive mate offering these benefits, implying a fixed preference shared by all. Countering this perspective, several reviews have highlighted the considerable variation in mate preferences that exists between individuals (Jennions and Petrie 1997; Widemo and Sæther 1999; Cotton et al. 2006; Ryan et al. 2007). Some of this may reflect variation in environmental factors (context-dependent variation; e.g., Milinski and Bakker 1992; Hedrick and Dill 1993), but even under the same circumstances, preferences are not uniform. Although there may be an average preference for a particular phenotype in the opposite sex, some individuals prefer this phenotype more strongly than others (i.e., they differ in choosiness) and some may even favor a different phenotype altogether (i.e., they differ in preference function). What explains this variation?

Preferences and/or choosiness may vary if individuals select their mates on the basis of genetic (e.g., based on the major histocompatibility complex) or phenotypic (e.g., size-based) compatibility (Jennions and Petrie 1997; Widemo and Sæther 1999; Bleay and Sinervo 2007). In these situations, the ideal mate for one individual will not be the same as the ideal mate for another individual. A different possibility is that individuals may have different preferences for purely strategic reasons, based on their own phenotypic condition and how this influences their success in the social environment. Phenotypic condition will be important in this context for 2 main reasons. First, it influences competitive ability, which determines an individual's success in intrasexual interactions. Previous theoretical work predicts that poor competitors should be less choosy because they cannot afford the costs of defending high-quality mates against stronger rivals; under intense competition, they may even reject such mates (Fawcett and Johnstone 2003; Härdling and Kokko 2005), as shown in orb-weaving spiders (Bel-Venner et al. 2008). Second, phenotypic condition influences attractiveness to the opposite sex, which determines success in intersexual interactions. Among species with mutual choice, unattractive individuals should be less choosy because only low-quality mates are likely to accept them (Gibson and Langen 1996; Johnstone 1997). In support of these predictions, several empirical studies have shown that attractive individuals or individuals in good condition are choosier (e.g., Kraak and Bakker 1998; Itzkowitz and Haley 1999; Amundsen and Forsgren 2003; Hunt et al. 2005; Burley and Foster 2006). Humans, for example, are more selective in partner choice if they consider themselves to be highly attractive (Pawłowski and Dunbar 1999; Little et al. 2001; Buston and Emlen 2003; Todd et al. 2007). Clearly, mate preferences are often not fixed and uniform but flexible and condition dependent (Cotton et al. 2006; Ryan et al. 2007).

Theoreticians have investigated condition-dependent mate preferences by allowing variation in quality in both sexes (e.g., Parker 1983; McNamara and Collins 1990; Real 1991; Johnstone 1997; Bergstrom and Real 2000; Fawcett and Johnstone 2003; Alpern and Reyniers 2005; Härdling and Kokko 2005). All these models assume that individuals "know" their own quality, in the sense that their mate-choice strategy can be based directly on it. This implies either that variation in quality is largely genetic and selection has coadapted preferences to this variation or that individuals can assess their own quality directly (e.g., via physiological cues) and employ a conditional mate-choice strategy based on this self-assessment. However, stochastic influences on development mean that quality is typically unpredictable and accurate self-assessment may not always be possible. In the face of this uncertainty, how should individuals decide on their level of choosiness?

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An obvious source of information on an individual's own attractiveness is the responses it gets from potential mates—specifically, whether they accept or reject him/her. In species with mutual choice, individuals should therefore be selected to learn from their previous experiences with the opposite sex. To date, however, models incorporating learning have largely been restricted to cases of 1-sided choice, as a means by which individuals assess the distribution of mate qualities (Dombrovsky and Perrin 1994; Mazalov et al. 1996; Collins et al. 2006). Only one published study, a series of computer simulations by Todd and Miller (1999), has considered mutual mate-choice strategies when individuals do not know their own attractiveness. The most successful strategy in their simulations, in terms of the number of individuals finding a mate and the degree to which that mate's quality matched their own, was "adjust relative/2." This strategy adjusts its aspirations for a mate according to its experiences during adolescence, becoming more choosy when accepted by a potential mate who exceeds its aspirations and less choosy when rejected by a potential mate below its aspirations. The simulations of Todd and Miller were an important first step in investigating the problem, but given that they considered only a small set of strategies, it is likely that others would outperform adjust relative/2. Furthermore, as the authors themselves acknowledged, their criteria for comparing the strategies were not the most evolutionarily relevant. Their approach did not address whether any of the strategies would be resistant to invasion by other mutant strategies, a necessary condition of evolutionary stability (Maynard Smith 1982).

Here, we extend the work of Todd and Miller (1999) by constructing a dynamic model of mutual mate choice in which individuals do not know their own quality. We calculate the fitness of different mate-choice strategies and use a stepwise algorithm to introduce rare mutants, gradually evolving a stable strategy that is resistant to invasion by alternative strategies.

THE MODEL

Outline of the model

Our model treats mutual mate choice as a dynamic game and is loosely based on the model developed by Johnstone (1997). We consider a large, stable population with a 1:1 sex ratio in which both males and females vary in quality, q, which can take integer values between 1 and $q_{\max}$. Here, an individual's quality is their value to the opposite sex as a mate; the fitness pay-off received from mating with a given partner is equal to that partner's value of q. In line with Johnstone, we assume a hump-shaped (specifically quartic) distribution for q in each sex, where the frequency of individuals of quality q is equal to $q^2(q-q_{\max}-1)^2$ divided by the total number of individuals of that sex. Thus, individuals of intermediate quality are abundant, whereas those of extremely high or extremely low quality are rare. Other distributions (e.g., uniform) give qualitatively similar results, but we do not present these here.

Individuals search for mates in a breeding season divided into T discrete time steps. At the start of each time step, males and females without a mate randomly pair up. Each member of a pair then independently decides whether or not to accept the current candidate partner. If both the male and the female consent, the pair drop out of the breeding pool and mate, each receiving a fitness pay-off equal to their partner's quality. They do not return to the breeding pool and therefore each individual can mate only once. If one or both parties decline the opportunity to mate with the current candidate, both individuals are unpaired at the start of the next time step and are free to continue sampling mates. Each additional round of sampling (i.e., each additional time step spent in the game) entails a fixed, additive fitness cost c, reflecting the energy spent searching for mates. In the penultimate time step ($T-1$), all unmated individuals are assumed to accept their current candidate because there is no opportunity for further sampling (no sampling takes place in time step T).

To narrow our search for adaptive mate-choice strategies, we assume that individuals adopt a "threshold" rule (Real 1990), whereby all candidate mates whose quality meets or exceeds a certain threshold are accepted whereas all those below it are rejected. This makes sense because 1) the fitness pay-off from mating increases with the partner's quality and 2) there is no possibility for individuals to be supplanted from their chosen mate (cf., Fawcett and Johnstone 2003); so if, in a given time step, a candidate of a specified quality is deemed acceptable, then all candidates of higher quality should also be acceptable. Threshold rules have previously been shown to be evolutionarily stable in a mutual choice setting (McNamara and Collins 1990).

Mate-choice strategies are specified by the function $a(t, x)$, where a is the minimum quality of an acceptable mate (i.e., the threshold; $1 \leq a \leq q_{\max}$) and is dependent on the time step, t (where $t = 1, 2, \ldots, T-1$), and a variable x which represents the experience gained by the individual in earlier time steps (see below). So, in the absence of errors, an individual in time step t with experience x will agree to mate if the quality of their current candidate is a or greater but will decline to mate if the quality is less than a. However, we assume that these acceptance decisions are error prone, with errors most likely for candidates close to the acceptance threshold. Specifically, the probability ε that an individual executes his/her decision wrongly is given by the logistic function

$$\varepsilon(a, q') = \frac{\varepsilon_{\max}}{1 + \exp(\beta|a - q'| - \alpha)}, \quad (1)$$

where a is his/her acceptance threshold, q' is the quality of the current candidate, $\varepsilon_{\max}$ is a constant determining the maximum chance of an error (ε is closest to $\varepsilon_{\max}$ when $q' = a$) and α and β are constants scaling the drop in the error rate as q' gets further from a (in all the results shown below, $\alpha = 5$ and $\beta = 2$). Individuals mistakenly accept a mate below their threshold with a frequency ε and correctly reject them with a frequency $(1 - \varepsilon)$; similarly, they mistakenly reject a mate at or above their threshold with a frequency ε and correctly accept them with a frequency $(1 - \varepsilon)$.

Note that the individual's own quality is not an argument for the choice function $a(t, x)$. Thus, in contrast to existing models of mate choice, the individuals in our model cannot directly perceive their own quality and are therefore initially unaware of their ability to attract the opposite sex. Instead, they rely on their previous experience in the mate-search game to glean information on their own attractiveness. We consider 3 simple types of experience an individual might use in making mate-choice decisions: (i) the number of times he/she has been accepted by a potential mate (hereafter, number of acceptances); (ii) the highest quality of a potential mate who has accepted him/her (quality of best acceptor); and (iii) the lowest quality of a potential mate who has rejected him/her (quality of worst rejector). In all the 3 cases, this experience is recorded by the integer variable x. For item (i), $x = 0, 1, \ldots, t-1$; for items (ii) and (iii), $x = 0, 1, 2, \ldots, q_{\max}$ (where $x = 0$ indicates no experience of acceptance or rejection, respectively).

Evolving the mate-choice strategy

We evolved the mate-choice strategy by iterating a simplified process of mutation and selection, until this gave a stable solution. In the results shown below, our starting point was the strategy $a(t, x) = 1$ for all t and all x, which implies that individuals are not choosy and simply accept the first candidate they meet. Other starting strategies gave slightly different outcomes, with changes in choosiness sometimes occurring at later time steps, but the evolved acceptance thresholds did not differ by more than one unit for any state (i.e., for any combination of t and x). The qualitative patterns were the same regardless of the starting point.

At each step of the iteration, we assumed that the "resident" strategy a was adopted by all members of the population, except for a single individual playing an alternative "mutant" strategy a^*. We calculated the expected fitness for the resident strategy and for each of a small set of possible mutant individuals that differed slightly from the resident (see below). If the fitness of the resident strategy exceeded that of all these mutants, it was retained as the resident, but otherwise, it was replaced by the fittest mutant (i.e., the mutant strategy became the new resident). In either case, a different set of mutants were picked for the next iteration. We halted the process when the resident strategy outperformed all the sets of mutants considered or if the number of iterations exceeded 10 000. Below we describe the steps involved in more detail.

Step 1: calculating the state-dependent frequency distribution for the resident population

For either sex, the frequency of individuals finding a mate of quality q' in time step t can be written as $f_{\mathrm{mate}}(t, q')$. Given a particular resident strategy, we used the calculations detailed in Appendix A to compute the expected frequencies of individuals mating with partners of different qualities in each time step. This involved calculating the expected frequencies of random encounters between unpaired males and females in different states and the probabilities that these individuals would agree to mate as specified by the resident strategy.

Step 2: calculating the expected fitness of the resident strategy

On mating, individuals receive a fitness pay-off W equal to the quality of their mate minus the search costs incurred in previous time steps. That is,

$$W(t, q') = q' - (t-1)c, \tag{2}$$

where t is the time step and q' is the quality of their mate; recall that their own quality q is unknown. To obtain the expected fitness of the resident strategy a, we computed an average of these fitness pay-offs weighted by the corresponding expected frequencies from the frequency distribution calculated in Step 1. Formally,

$$\hat{W}(a) = \sum_{t=1}^{T-1} \sum_{q'=1}^{q_{\max}} f_{\mathrm{mate}}(t, q') \cdot W(t, q'), \tag{3}$$

where $\hat{W}(a)$ denotes the expected pay-off for an individual playing strategy a. (Because all individuals mate at some point, we do not need to consider $q' = 0$ in this weighted average.)

Step 3: generating the mutant strategies

To allow the mate-choice strategy to evolve gradually, we considered only small mutations in the resident strategy, changing its acceptance thresholds one at a time. In a given iteration of our evolutionary process, we selected a single combination of values of t ($t = t_{\mathrm{m}}$) and x ($x = x_{\mathrm{m}}$) and adjusted the corresponding acceptance threshold $a(t_{\mathrm{m}}, x_{\mathrm{m}})$ up or down by 1 or 2 units (for details of how we selected t_{m} and x_{m}, see Step 6, below). Thus, we considered 4 possible mutants: $a^*(t_{\mathrm{m}}, x_{\mathrm{m}}) = a(t_{\mathrm{m}}, x_{\mathrm{m}}) + 1$, $a^*(t_{\mathrm{m}}, x_{\mathrm{m}}) = a(t_{\mathrm{m}}, x_{\mathrm{m}}) + 2$, $a^*(t_{\mathrm{m}}, x_{\mathrm{m}}) = a(t_{\mathrm{m}}, x_{\mathrm{m}}) - 1$ and $a^*(t_{\mathrm{m}}, x_{\mathrm{m}}) = a(t_{\mathrm{m}}, x_{\mathrm{m}}) - 2$ (but always within the limits $1 \leq a^* \leq q_{\max}$). For all other values of t and x, the acceptance thresholds of the resident and mutant were identical (i.e., $a^*(t, x) = a(t, x)$).

Step 4: calculating the expected fitness of the mutant strategies

For each of these 4 mutants, we calculated the expected fitness for a single individual playing the mutant strategy a^* in a population of individuals playing the resident strategy a. To do this, we needed to obtain a distribution of probabilities $p_{\mathrm{mate}}(t, q')$ that a mutant individual (of unknown quality) ends up with a mate of quality q' in time step t. These probabilities were determined by the frequency distribution computed in Step 1 (Appendix A) and the chances of mutual acceptance at each encounter, according to the mutant and resident strategies a and a^*. We assumed that the mutant individual's quality is drawn from the same quartic distribution as the resident and that it is error prone in the same way (as specified by Equation 1). The full calculations are given in Appendix B. Assuming the same pay-off function as for the resident (Equation 2), we could then calculate the expected fitness of the mutant as a weighted average,

$$\hat{W}(a^*) = \sum_{t=1}^{T-1} \sum_{q'=1}^{q_{\max}} p_{\mathrm{mate}}(t, q') \cdot W(t, q'). \tag{4}$$

Step 5: updating the resident strategy

If the expected fitness of the resident exceeded that of all 4 mutants ($\hat{W}(a) > \hat{W}(a^*)$ for all a^*), it remained the resident strategy in the next iteration. Otherwise ($\hat{W}(a) \leq \hat{W}(a^*)$ for at least one a^*), the mutant with the highest fitness "invaded" the population to become the new resident strategy for the next iteration. Thus, not only mutants of higher fitness but also those of equal fitness could displace the resident strategy.

Step 6: iterating until convergence

Steps 1–5 were carried out repeatedly, allowing gradual evolution of the mate-choice strategy through small mutations in the acceptance thresholds, one at a time. We cycled through the set of acceptance thresholds in a fixed order, starting with $t_{\mathrm{m}} = 1$ and $x_{\mathrm{m}} = 0$ (i.e., the threshold $a(1, 0)$) in the first iteration, then $t_{\mathrm{m}} = 2$ and $x_{\mathrm{m}} = 0$ in the second iteration, then $t_{\mathrm{m}} = 2$ and $x_{\mathrm{m}} = 1$ in the third iteration, and so on until $t_{\mathrm{m}} = T - 1$ and $x_{\mathrm{m}} = T - 2$ (for number of acceptances) or $x_{\mathrm{m}} = q_{\max}$ (for quality of best acceptor/worst rejector), at which point we returned to the start of the sequence. When we could cycle through the entire set of acceptance thresholds (i.e., all possible of values of t_{m} and x_{m}) without finding a single mutant of equal or higher fitness, this indicated that a stable solution had been reached. The mate-choice strategies evolved in this way are locally rather than globally stable (because we considered only small mutation steps), but the conditions for stability were strict in that we allowed neutral mutants to invade. There was no guarantee that the iterative process would actually converge on a stable solution. If convergence did not occur, we terminated the process after 10 000 iterations.

The approach described is computationally intensive, so we implemented it in a programming language (Pascal). Copies of the code are available from the authors on request. Because we assumed a 1:1 sex ratio, one mate per individual and the same initial frequency distribution of qualities in both sexes, the mate-choice strategies are identical for males and females. The results we describe therefore hold for both sexes.

RESULTS

We considered a breeding season of 20 time steps ($T = 20$) and a range of 10 different qualities ($q_{\max} = 10$). Except for when they were being manipulated, default values for the sampling cost and error parameters were $c = 0.05$ and $\varepsilon_{\max} = 0.2$ (α and β, controlling the drop in error rate away from the threshold, were held at $\alpha = 5$ and $\beta = 2$). All the results shown below evolved from a nonchoosy starting strategy of $a(t, x) = 1$ for all t and x. Different starting points gave slightly different results, but the qualitative patterns were the same.

Evolved acceptance thresholds

The evolved acceptance thresholds are depicted in Figure 1 for the 3 different types of experience we considered. When x was the number of acceptances (Figure 1a), the evolutionary process converged on a stable solution after 2635 iterations, in which 555 changes were made to the resident strategy. When x was the quality of the best acceptor (Figure 1b), a stable solution was reached after 5252 iterations and 786 changes. For the quality of the worst rejector, however, no stable solution was reached overall: Although nearly all of the acceptance thresholds settled on a fixed value, 2 (out of 191) continued to alternate between adjacent values (Figure 1c, unstable thresholds indicated by crosses). Nonetheless, the pattern seen in the acceptance thresholds which did stabilize is broadly comparable to that for the other types of experience.

The highest threshold adopted by the evolved strategy is $a = 7$ when x records the number of acceptances (Figure 1a) or the quality of the best acceptor (Figure 1b) and $a = 6$ when x records the quality of the worst rejector (Figure 1c). Individuals whose quality meets or exceeds this threshold are therefore acceptable to all mates in all time steps of the breeding season. As predicted by earlier models of mate choice (e.g., Real 1990; Johnstone 1997), choosiness declines over time, with the threshold falling as the end of the breeding season approaches. This reflects the costs of continued searching and the increasing risk of ending up unpaired. An exception to this general pattern is seen for the quality of the worst rejector (Figure 1c), where for $x \geq 6$, choosiness first increases before decreasing. Johnstone (1997) also observed an initial increase in choosiness, which he ascribed to sampling costs, but he saw it only for poor-quality individuals, and this does not seem to account for our own result because high values of x tend to be experienced by higher-quality individuals (see below). We do not have a clear explanation for this pattern, but we stress that it also emerged when we ran our algorithm from other starting points and seems to be a robust feature of the evolved mate-choice strategy when individuals keep track of the quality of the worst rejector. We also see 2 brief, unexpected increases in choosiness when x records the quality of the best acceptor, at $t = 10$, $x = 3$ and $t = 17$, $x = 0$. The fitness effects of these increases are tiny, however, so this probably reflects a rounding error in our algorithm.

Higher values of the sampling cost c generate an evolved strategy with lower acceptance thresholds (results not shown) because the expected pay-off from continuing to search for a mate is reduced. This effect has been found in previous models of mate choice (e.g., Johnstone 1997; Collins et al. 2006). Raising the error rate (by increasing the value of $\varepsilon_{\max}$) has a similar effect on the favored strategy, with individuals reducing their choosiness when errors are common (results not shown). In this situation, the acceptance and rejection decisions of others are less informative, so there is little to be gained from an extended period of sampling potential mates.

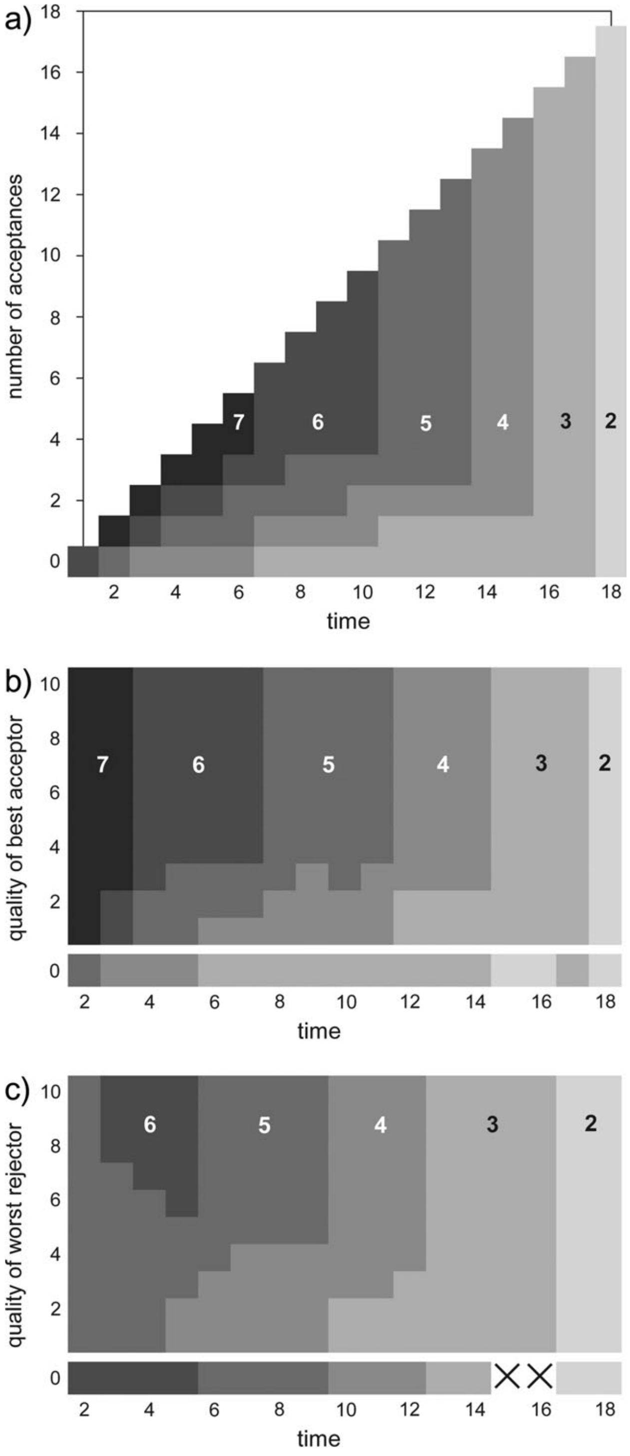

Figure 1
Evolved acceptance thresholds when individuals keep track of (a) the number of acceptances, (b) the quality of the best acceptor, or (c) the quality of the worst rejector (see text for details). In (b) and (c), the lower bar for quality 0 represents the strategy for individuals that have not yet been accepted or rejected, respectively. Parameter values are given in the main text. Numbers on the plots give the acceptance thresholds, with darker shading indicating higher choosiness. In (c), the crosses indicate acceptance thresholds that did not converge on a stable value, instead alternating between 2 and 3.

Our original question concerned the effect of previous experiences on mate preferences. For all versions of the model, the acceptance thresholds of the evolved strategy change with experience. Depending on the information retained, the acceptance threshold increases with number of acceptances (Figure 1a), with the quality of the best acceptor (Figure 1b) or with the quality of the worst rejector (Figure 1c). Thus, individuals should be more choosy if they have been accepted by more of the potential mates they meet, if they have been accepted by a higher-quality mate, or if they have never been rejected by lower-quality mates. In all cases, the favored strategy is sensitive to previous experiences and adjusts its choosiness accordingly. Because this flexible strategy emerged from a fixed threshold rule with which we began the evolutionary process, it evidently has a selective advantage over strategies that are blind to previous experiences.

Experiences of acceptance and rejection

Why should individuals respond to previous experiences in this way? The reason is straightforward: an individual's history of acceptance or rejection by potential mates is a cue to their own quality. From the chances of encountering different candidate mates and being accepted or rejected under the resident strategy $a(t, x)$, we calculated the average experience of individuals still searching for a mate at each time step of the game. Figure 2 shows this average experience for unmated individuals of different qualities q (the value of q being unknown to themselves), in terms of the mean number of acceptances per time step (Figure 2a), mean quality of best acceptor (Figure 2b), and mean quality of worst rejector (Figure 2c). In all 3 cases, there is a clear, monotonic relationship between experience and quality: Individuals of higher quality are accepted more frequently than those of lower quality, they are accepted by higher-quality individuals, and any rejections they suffer tend to come from higher-quality individuals. Even individuals of quality $q \geq 7$, who are acceptable to all mates in all time steps, experience different histories of acceptance and rejection depending on their precise value of q. This is because the chance of errors decreases with distance from the acceptance threshold, such that individuals of quality $q = 10$ are less likely to be rejected than those of quality $q = 9$, who in turn are less likely to be rejected than those of quality $q = 8$, who in turn are less likely to be rejected than those of quality $q = 7$.

To sum up, the number of acceptances, the quality of the best acceptor, and the quality of the worst rejector are all reliable cues on which to base one's choosiness. For the remainder of the results, however, we focus on the case where x records the number of acceptances because this gave the clearest relationship between experience and choosiness.

Assortative mating

Figure 3 shows the frequency distribution of unmated individuals of different qualities at each time step of the mate-search game. Individuals of quality $q \geq 7$, who are universally acceptable from time step $t = 1$ onwards, drop rapidly in frequency as they pair up and become unavailable for further mating. Individuals of lower qualities initially mate only through error, then drop out more quickly when they first become acceptable to a subset of the population. Over time, the frequency distribution of unmated individuals becomes increasingly skewed toward lower qualities.

This pattern suggests that mating is broadly assortative. We would expect to see assortative mating even if individuals adopted a simple time-dependent threshold that ignored previous experiences; high-quality individuals should pair up first through mutual acceptance, whereas lower quality individuals remain in the mating pool until they first become acceptable. Does learning from experience make this pattern more assortative? To answer this question, we compared the degree of assortative mating in our basic model with that found under 2 alternative scenarios: 1 in which individuals are directly sensitive to their own quality q (i.e., their acceptance thresholds are specified by the function $a(t, q)$), as assumed in most standard models of mate choice, and 1 in which individuals are ignorant of their own quality and also unable to respond to their previous experiences (i.e., their acceptance thresholds, $a(t)$, depend only on the time step). For each scenario, we evolved the mate-choice strategy as detailed above and then quantified the resulting strength of assortative mating by calculating the Pearson correlation coefficient between male and female qualities across all mated pairs. These correlation coefficients are plotted against time in Figure 4.

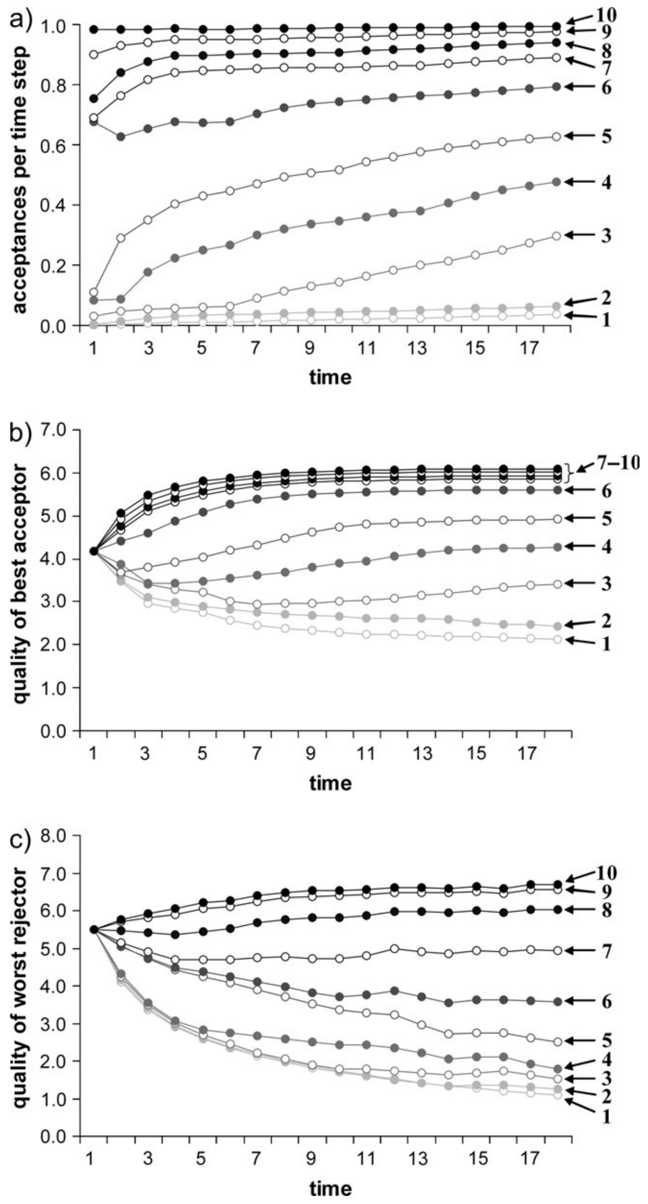

Figure 2
Mean values of the experience variable x for unpaired individuals of different quality q (which is unknown to them), when x represents (a) the number of acceptances (here divided by the number of time steps), (b) the quality of the best acceptor, or (c) the quality of the worst rejector (see text for details). The numbered arrows indicate the quality values (q). Parameter values are given in the main text.

In our basic model, where individuals are ignorant of their own quality but keep track of the number of times they have been accepted, the degree of assortative mating rises rapidly over time as individuals gain experience, culminating in a correlation of $r = 0.549$ in the final time step. In contrast, when

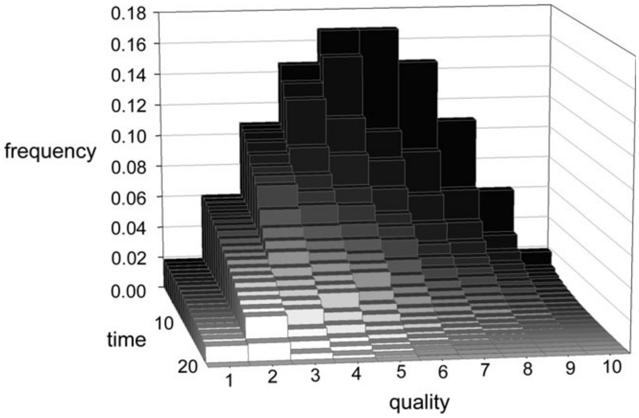

Figure 3
The frequency of unmated individuals of each quality over time for a mate-choice strategy that is sensitive to the number of acceptances received in earlier time steps. The initial frequencies follow a quartic distribution (see main text) for which the total frequency sums to 1. In the final time step ($t = 20$), all remaining individuals mate. Parameter values are given in the main text.

choosiness is directly sensitive to quality, the correlation between male and female qualities is high from the very first time step. Thereafter, it stays at roughly the same level, ending up at a value of $r = 0.687$, higher than that for our basic model. The third situation, in which individuals are ignorant of their own quality and cannot recall the outcome of their previous interactions, leads to weaker assortative mating, with a final correlation of $r = 0.417$ between male and female qualities. So, by learning from their previous experiences, individuals that are ignorant of their own quality can considerably enhance the degree of assortative mating.

DISCUSSION

Fixed versus flexible choosiness

For all types of experience we considered, the favored strategy we found was one in which individuals are sensitive to acceptances and rejections by potential mates and adjust their choosiness accordingly. If an individual is uncertain of its own quality, it therefore pays to respond to the decisions of others rather than adopting a fixed acceptance threshold that depends only on the time step. Generally speaking, "positive" experiences, namely frequent acceptance or acceptance by high-quality mates, tend to increase choosiness, whereas "negative" experiences, namely frequent rejection or rejection by low-quality mates, tend to decrease choosiness. At this qualitative level, our evolved strategy shows similar behavior to adjust relative/2, which was the most successful strategy in the computer simulations of Todd and Miller (1999). The evolved strategy responds more flexibly than adjust relative/2, however, in that the amount by which it adjusts its choosiness is dependent on the time step. The route we took to find this strategy, starting from a fixed threshold in all states, suggests that it could easily evolve from a population in which individuals are insensitive to feedback from the opposite sex.

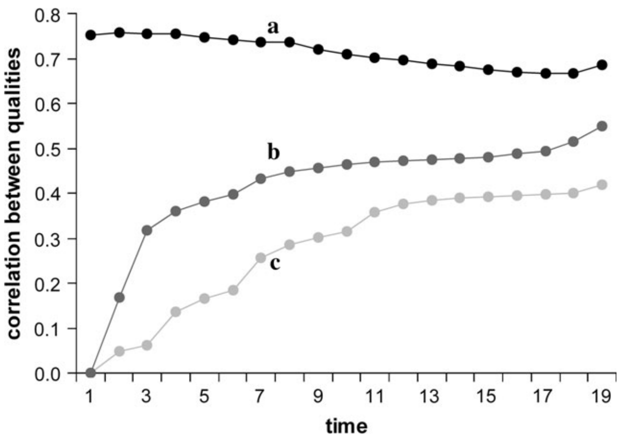

Figure 4
The strength of assortative mating under 3 different scenarios: (a) individuals know their own quality, (b) individuals do not know their own quality but can respond to previous experiences, and (c) individuals do not know their own quality and cannot respond to previous experiences. The values shown are the Pearson correlation coefficients between the male and female qualities for all mated pairs formed up to and including the corresponding time point. Parameter values are given in the main text.

Our findings lend further support to the idea that mate preferences might often be flexible and state dependent rather than fixed traits shared by all individuals (Jennions and Petrie 1997; Widemo and Sæther 1999; Cotton et al. 2006; Bleay and Sinervo 2007; Ryan et al. 2007). Holding out for the best mates may be an unrealistic strategy for low-quality individuals because they are unlikely to be accepted by those mates (Gibson and Langen 1996; Johnstone 1997) or unable to access them by outcompeting highly competitive rivals (Fawcett and Johnstone 2003; Härdling and Kokko 2005). Instead, by adjusting their preferences to their own quality, individuals can employ a more prudent mate-choice strategy tuned to their prospects on the mating market (Härdling and Kokko 2005). We should therefore expect an animal's mate-choice behavior to be sensitive to cues of its own attractiveness, whether perceived directly or via the responses of others. The main message of our paper is that social feedback, in terms of success in previous interactions with the opposite sex, can be an important part of this.

Our model predicts that individuals will be sensitive to previous experiences when they are uncertain of their own quality. For example, where unpredictable, stochastic factors exert a strong influence on development, and individuals have limited capacity to perceive their own state directly (e.g., via physiological cues), acceptances and rejections from the opposite sex might be the most useful source of information on which to base choosiness. In other situations, individuals may be able to base their mate-choice behavior directly on their own quality without the need to sample mates first. One way this might happen is if variation in quality and choosiness is largely genetic, in which case selection could potentially generate genetic covariation in which high-quality individuals are choosy and low-quality individuals less so. Alternatively, if there are reliable physiological correlates of quality to which individuals can directly respond, then selection could favor state-dependent choosiness based on those correlates even when quality shows little genetic variation. However, regardless of the mechanisms involved, individuals are unlikely to be able to perceive their own attractiveness with perfect accuracy, so sensitivity to previous experiences may play an important role in fine-tuning mate preferences.

Empirical tests

The predictions of our model apply to species with mutual mate choice and could be tested in any such system where it is possible to manipulate the amount of interest received from the opposite sex. Standard choice tests could be used to assess the choosiness of the experimental subjects before and after receiving high or low levels of interest. We predict no effect on choosiness in species where only one sex is choosy because individuals of that sex are equally attractive to potential mates and should therefore not have been selected to respond to changes in mating interest. Among species with mutual choice, where both males and females risk being rejected by the opposite sex, we expect that sensitivity to previous experiences will be taxonomically widespread. This is based on the fact that the strategies in our model relied on rather simple information to adjust their choosiness, suggesting that such flexible mate-choice behavior does not require sophisticated cognitive abilities.

Experimental studies confirm that choosiness is affected by previous experiences in a variety of taxa, including sticklebacks (*Gasterosteus aculeatus*; Bakker and Milinski 1991), sculpins (*Cottus bairdi*; Downhower and Lank 1994), zebra finches (*Taeniopygia guttata*; Collins 1995), field crickets (*Gryllus bimaculatus*; Bateman et al. 2001), and fruit flies (*Drosophila melanogaster*; Dukas 2005). In each of these studies, females courted by a male with an attractive phenotype subsequently showed a stronger preference for that phenotype than females courted by an unattractive male. However, this result does not distinguish between the effects of being courted by an attractive male and merely being exposed to such a male, so does not address our central prediction that interest from the opposite sex should influence choosiness. Instead, the female's previous encounter could simply give her an indication of the quality of locally available males; when this is found to be high, it pays her to be more choosy (Dombrovsky and Perrin 1994; Mazalov et al. 1996; Collins et al. 2006). To exclude this possibility, it would be necessary to expose subjects to mates with the same range of phenotypes, manipulating only the interest shown by those mates.

Parallels with winner and loser effects

The impact of acceptances and rejections on choosiness is analogous to the winner and loser effects commonly seen in animal contests (reviewed by Hsu et al. 2006; Rutte et al. 2006), in which the experience of winning makes a contestant more likely to win a subsequent fight, whereas the experience of losing makes it more likely to lose. Indeed, one explanation proposed for winner and loser effects is that experiences in previous fights enable an individual to assess its own fighting ability relative to others (Whitehouse 1997; Hsu and Wolf 1999; Mesterton-Gibbons 1999), the so-called "self-assessment hypothesis." In our model of mutual mate choice, individuals alter their choosiness for a similar reason: This helps them to adopt an appropriate level of choosiness given their attractiveness to the opposite sex, just as experience in contests might help individuals to adopt an appropriate level of aggression given their relative fighting ability.

Limitations and possible extensions

Our model assumes that, although ignorant of their own quality, individuals can judge the quality of potential mates without error. This is unlikely to be the case in real systems and it would be interesting to relax this assumption, so that individuals make assessment errors as well as errors in executing their decisions (Johnstone and Grafen 1992; Wiegmann and Angeloni 2007). For the sake of simplicity, we also assumed that the distribution of qualities in both sexes was fixed, such that the mate-choice strategies could adapt fully to this. In variable environments, this assumption is unlikely to hold. Other authors (e.g., Dombrovsky and Perrin 1994; Mazalov et al. 1996; Collins et al. 2006) have modeled mate-choice strategies when the distribution of qualities in the opposite sex is uncertain, showing that strategies which learn about the local distribution as they sample typically outperform fixed threshold rules. However, to our knowledge, no one has considered the effect of uncertainty about the quality distribution in one's own sex. This is important because even if an individual knows its own quality perfectly, this may not be enough for a successful mate-choice strategy: Its attractiveness to the opposite sex depends critically on the qualities of other individuals of the same sex (Noë and Hammerstein 1995; Todd and Miller 1999). Such uncertainty could conceivably result in the same kind of behavior seen in our current model, where individuals rely on their previous experiences with the opposite sex to set their level of choosiness. Or the solution could be more complicated, particularly if the quality distribution in the opposite sex is simultaneously unknown. This would be a useful direction for future work.

Ultimately, the range of possible strategies we considered was constrained by the type of experience individuals retained in each version of the model. Owing to computational limitations, we restricted our analysis to very simple types of experience which kept the strategy set of acceptance thresholds manageable. It is conceivable, and even likely, that more sophisticated strategies would do even better, for example, by using a combination of the types of experience investigated here (e.g., number of acceptances in conjunction with quality of best acceptor) or some other metric such as the median quality of acceptors (or rejectors). In no way does this alter our essential point: When individuals are uncertain of their own quality, responding even to very simple information can be better than blindly using a threshold which drops over time but ignores feedback from potential mates.

APPENDIX A

Calculating the expected frequencies resulting from the resident strategy

Here, we outline the frequency calculations for the case where x records the number of acceptances an individual has experienced in earlier time steps. For the other types of experience we considered (quality of best acceptor, quality of worst rejector), the updating of x is different but otherwise the principles are the same. We describe the steps involved by taking the female's point of view, but the same logic applies for calculating the frequencies of males.

At the start of any given time step t, we can write the expected frequency, f, of females of quality q and past number of acceptances x, mated to a male of quality q', as $f(t, q, x, q')$. If the female has not yet mated ($q' = 0$), she is free to continue searching for a partner. Assuming random assortment, the chance, $p_{\text{candidate}}$, that the next male she encounters is of quality q' and has been accepted x' times is given by

$$p_{\text{candidate}}(t, q', x') = \frac{f(t, q', x', 0)}{\sum_{q=1}^{q_{\max}} \sum_{x=0}^{t-1} f(t, q, x, 0)}, \tag{A1}$$

where $f(t, q', x', 0)$ is the frequency of such males and the denominator gives the total frequency of unmated males, summed across all qualities and experiences (note that this equals 1 in the first time step but declines thereafter, as males pair up and drop out of the breeding pool). Out of all females in the population, the frequency, f_{meet}, of females of quality q and experience x encountering a male of quality q' and experience x' in time step t is therefore

$$f_{\mathrm{meet}}(t,q,x,q',x') = f(t,q,x,0)\cdot p_{\mathrm{candidate}}(t,q',x'). \tag{A2}$$

These encounter frequencies are simple to obtain for the first time step ($t = 1$), where all individuals are unmated ($q = q' = 0$) and lack experience ($x = x' = 0$) and their initial frequencies $f(1, q, 0, 0)$ are known from a specified distribution.

Using the encounter frequencies for various combinations of q, x, q', and x', we can work out the frequencies of mated and unmated individuals at the start of the next time step, according to the chances that one or both parties will accept or reject the other. This depends on the qualities of the female (q) and the male (q'), their acceptance thresholds (a) under the resident strategy, and the error rate (ε). First, consider an unmated female at the start of the next time step, $t + 1$, with quality q and number of acceptances x. To end up in this situation, 1 of 3 things must have happened during the previous time step (t):

(i) The female accepted the male, but the male rejected the female; so the female's number of acceptances prior to that encounter was x. If $q' < a(t, x)$ and $q < a(t, x')$, this happened with probability $\varepsilon(a, q')\cdot(1-\varepsilon(a, q))$ (the female made an error but the male did not); if $q' \geq a(t, x)$ and $q < a(t, x')$, it happened with probability $(1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q))$ (neither individual made an error); if $q' < a(t, x)$ and $q \geq a(t, x')$, it happened with probability $\varepsilon(a,q')\cdot\varepsilon(a,q)$ (both individuals made an error); and if $q' \geq a(t, x)$ and $q \geq a(t, x')$, it happened with probability $(1-\varepsilon(a,q'))\cdot\varepsilon(a,q)$ (the male made an error but the female did not). In all cases, the female begins the next time step ($t + 1$) with her number of acceptances still at x.

(ii) The male accepted the female, but the female rejected the male; so the female's number of acceptances prior to that encounter was $x - 1$. If $q' < a(t, x - 1)$ and $q < a(t, x')$, this happened with probability $(1-\varepsilon(a,q'))\cdot\varepsilon(a,q)$ (the male made an error but the female did not); if $q' \geq a(t, x - 1)$ and $q < a(t, x')$, it happened with probability $\varepsilon(a,q')\cdot\varepsilon(a,q)$ (both individuals made an error); if $q' < a(t, x - 1)$ and $q \geq a(t, x')$, it happened with probability $(1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q))$ (neither individual made an error); and if $q' \geq a(t, x - 1)$ and $q \geq a(t, x')$, it happened with probability $\varepsilon(a,q')\cdot(1-\varepsilon(a,q))$ (the female made an error but the male did not). In all cases, the female begins the next time step ($t + 1$) with her number of acceptances updated to x.

(iii) The female and the male both rejected each other; so the female's number of acceptances prior to that encounter was x. If $q' < a(t, x)$ and $q < a(t, x')$, this happened with probability $(1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q))$ (neither individual made an error); if $q' \geq a(t, x)$ and $q < a(t, x')$, it happened with probability $\varepsilon(a,q')\cdot(1-\varepsilon(a,q))$ (the female made an error but the male did not); if $q' < a(t, x)$ and $q \geq a(t, x')$, it happened with probability $(1-\varepsilon(a,q'))\cdot\varepsilon(a,q)$ (the male made an error but the female did not); and if $q' \geq a(t, x)$ and $q \geq a(t, x')$, it happened with probability $\varepsilon(a,q')\cdot\varepsilon(a,q)$ (both individuals made an error). In all cases, the female begins the next time step ($t + 1$) with her number of acceptances still at x.

Collecting together these possibilities, we arrive at the frequency of unmated females of quality q and with number of acceptances x at the start of the next time step, $t + 1$:

$$\begin{aligned}
f(t+1,q,x,0) = {} & \varepsilon(a,q')\cdot(1-\varepsilon(a,q)) \sum_{q<a(t,x')}\ \sum_{q'<a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + (1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q)) \sum_{q<a(t,x')}\ \sum_{q'\geq a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + \varepsilon(a,q')\cdot\varepsilon(a,q) \sum_{q\geq a(t,x')}\ \sum_{q'<a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + (1-\varepsilon(a,q'))\cdot\varepsilon(a,q) \sum_{q\geq a(t,x')}\ \sum_{q'\geq a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + (1-\varepsilon(a,q'))\cdot\varepsilon(a,q) \sum_{q<a(t,x')}\ \sum_{q'<a(t,x-1)} f_{\mathrm{meet}}(t,q,x-1,q',x') \\
& + \varepsilon(a,q')\cdot\varepsilon(a,q) \sum_{q<a(t,x')}\ \sum_{q'\geq a(t,x-1)} f_{\mathrm{meet}}(t,q,x-1,q',x') \\
& + (1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q)) \sum_{q\geq a(t,x')}\ \sum_{q'<a(t,x-1)} f_{\mathrm{meet}}(t,q,x-1,q',x') \\
& + \varepsilon(a,q')\cdot(1-\varepsilon(a,q)) \sum_{q\geq a(t,x')}\ \sum_{q'\geq a(t,x-1)} f_{\mathrm{meet}}(t,q,x-1,q',x') \\
& + (1-\varepsilon(a,q'))\cdot(1-\varepsilon(a,q)) \sum_{q<a(t,x')}\ \sum_{q'<a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + \varepsilon(a,q')\cdot(1-\varepsilon(a,q)) \sum_{q<a(t,x')}\ \sum_{q'\geq a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + \varepsilon(a,q')\cdot(1-\varepsilon(a,q)) \sum_{q\geq a(t,x')}\ \sum_{q'<a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x') \\
& + \varepsilon(a,q')\cdot\varepsilon(a,q) \sum_{q\geq a(t,x')}\ \sum_{q'\geq a(t,x)} f_{\mathrm{meet}}(t,q,x,q',x').
\end{aligned} \tag{A3}$$

The paired sigma notation here indicates summation over x' and q' such that the specified conditions are met. The first 4 terms are associated with scenario (i) above (female accepted male, but male rejected female), the middle 4 with scenario (ii) (male accepted female, but female rejected male), and the last 4 with scenario (iii) (both individuals rejected the other).

Now consider a female of quality q who at the start of time step $t+1$ has number of acceptances x and is mated to a male of quality q'. How did she arrive in this state? One possibility is that she was already mated to him at the start of the preceding time step (t), when her number of acceptances was already at x; this is the case for a fraction $f(t, q, x, q')$ of females. Alternatively, she was unmated at the start of time step t but successfully obtained the male she encountered in that time step, simultaneously updating her number of acceptances from $x-1$ to x. If $q' < a(t, x-1)$ and $q < a(t, x')$, the chance of them both agreeing to mate was $\varepsilon(a, q') \cdot \varepsilon(a, q)$ (both made an error); if $q' \geq a(t, x-1)$ and $q < a(t, x')$, the chance was $(1-\varepsilon(a, q')) \cdot \varepsilon(a, q)$ (the male made an error but the female did not); if $q' < a(t, x-1)$ and $q \geq a(t, x')$, the chance was $\varepsilon(a, q') \cdot (1-\varepsilon(a, q))$ (the female made an error but the male did not); and if $q' \geq a(t, x-1)$ and $q \geq a(t, x')$, the chance was $(1-\varepsilon(a, q')) \cdot (1-\varepsilon(a, q))$ (neither individual made an error). Collecting together these possibilities, the frequency of females of quality q and with number of acceptances x, mated to a male of quality q' at the start of time step $t+1$, is

$$\begin{aligned} f(t+1, q, x, q') = {} & f(t, q, x, q') \\ & + \varepsilon(a, q') \cdot \varepsilon(a, q) \sum_{q < a(t,x')} \sum_{q' < a(t,x-1)} f_{\text{meet}}(t, q, x-1, q', x') \\ & + (1-\varepsilon(a, q')) \cdot \varepsilon(a, q) \sum_{q < a(t,x')} \sum_{q' \geq a(t,x-1)} f_{\text{meet}}(t, q, x-1, q', x') \\ & + \varepsilon(a, q') \cdot (1-\varepsilon(a, q)) \sum_{q \geq a(t,x')} \sum_{q' < a(t,x-1)} f_{\text{meet}}(t, q, x-1, q', x') \\ & + (1-\varepsilon(a, q')) \cdot (1-\varepsilon(a, q) \sum_{q \geq a(t,x')} \sum_{q' \geq a(t,x-1)} f_{\text{meet}}(t, q, x-1, q', x'). \end{aligned} \tag{A4}$$

The last 4 terms here deal with those females who obtained a mate in the preceding time step, whereas the first term takes account of those females who mated at an earlier stage.

In this way, we can calculate the frequencies of females in all states (i.e., all combinations of q, x, and q') at $t = 2$ from those at $t = 1$. We can do the same for males by reversing the roles and using the same set of Equations (A1–A4) because both sexes follow the same strategy (see main text). We then repeat the process to obtain the frequencies of individuals in all states at $t = 3$, and so on until $t = T-1$, when all unmated individuals are assumed to accept their current candidate without error. Thus, at the start of the final time step ($t = T$), there are no unmated individuals ($f(T, q, x, 0) = 0$ for any q and x), and the frequencies of mated individuals are given by

$$f(T, q, x, q') = f(T-1, q, x, q') + \sum_{x'=0}^{T-2} f_{\text{meet}}(T-1, q, x, q', x'). \tag{A5}$$

Finally, using the frequencies obtained in Equations A4 and A5, we can calculate the total frequency f_{mate} of individuals mating with a partner of quality q' in any given time step t. We do this by taking the frequencies of mated individuals up to that point and summing them over all qualities (q) and experiences (x), then subtracting those who had already mated in an earlier time step:

$$f_{\text{mate}}(t, q') = \sum_{q=1}^{q_{\max}} \left(\sum_{x=1}^{t-1} f(t, q, x, q') - \sum_{x=1}^{t-2} f(t-1, q, x, q') \right). \tag{A6}$$

It is these f_{mate} frequencies that are used to calculate the expected fitness of the resident strategy (see main text).

APPENDIX B

Calculating the probability distribution of mating outcomes for a mutant individual

The method to calculate the probability distribution of mating outcomes for a mutant individual is similar to that used to obtain the f_{mate} frequencies for the resident population (Appendix A). We can write the chance that the mutant is in a particular state at the start of time step t as $p(t, q^*, x^*, q')$, where q^* is its quality (unknown to itself), x^* is the number of times it has been accepted so far, and q' is the quality of its mate ($q' = 0$ for unmated individuals). Thus, the chance that the mutant finds itself unmated by the start of time step t, has (unknown) quality q^* and has been accepted x^* times, is $p(t, q^*, x^*, 0)$. Analogously to Equation A2, the chance it encounters a candidate of quality q' and experience x' in that time step is then

$$p_{\text{meet}}(t, q^*, x^*, q', x') = p(t, q^*, x^*, 0) \cdot p_{\text{candidate}}(t, q', x'). \tag{B1}$$

These encounter probabilities are simple to obtain for the first time step ($t = 1$), in which we know the probability distribution for the mutant's state, $p(1, q^*, 0, 0)$, and the chances of encountering different types of resident candidates can be determined from the initial frequency distribution of the resident population, $f(1, q', 0, 0)$.

For subsequent time steps, we use the same logic applied in Appendix A to consider the outcome of interactions between the mutant individual and the potential mates it encounters from the resident population. Mirroring Equation A3, the chance that the mutant remains unmated at the start of time step $t+1$, with (unknown) quality q^* and number of acceptances x^*, is

$$
\begin{aligned}
p(t+1,q^*,x^*,0) = {} & \varepsilon(a^*,q')\cdot(1-\varepsilon(a,q^*)) \sum_{q^*<a(t,x')} \sum_{q'<a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot(1-\varepsilon(a,q^*)) \sum_{q^*<a(t,x')} \sum_{q'\geq a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + \varepsilon(a^*,q')\cdot\varepsilon(a,q^*) \sum_{q^*\geq a(t,x')} \sum_{q'<a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot\varepsilon(a,q^*) \sum_{q^*\geq a(t,x')} \sum_{q'\geq a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot\varepsilon(a,q^*) \sum_{q^*<a(t,x')} \sum_{q'<a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + \varepsilon(a^*,q')\cdot\varepsilon(a,q^*) \sum_{q^*<a(t,x')} \sum_{q'\geq a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot(1-\varepsilon(a,q^*)) \sum_{q^*\geq a(t,x')} \sum_{q'<a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + \varepsilon(a^*,q')\cdot(1-\varepsilon(a,q^*)) \sum_{q^*\geq a(t,x')} \sum_{q'\geq a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot(1-\varepsilon(a,q^*)) \sum_{q^*<a(t,x')} \sum_{q'<a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + \varepsilon(a^*,q')\cdot(1-\varepsilon(a,q^*)) \sum_{q^*<a(t,x')} \sum_{q'\geq a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + \varepsilon(a^*,q')\cdot(1-\varepsilon(a,q^*)) \sum_{q^*\geq a(t,x')} \sum_{q'<a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x') \\
& + \varepsilon(a^*,q')\cdot\varepsilon(a,q^*) \sum_{q^*\geq a(t,x')} \sum_{q'\geq a^*(t,x^*)} p_{\text{meet}}(t,q^*,x^*,q',x').
\end{aligned}
\tag{B2}
$$

The first 4 terms here deal with cases where the mutant accepted the candidate mate in the preceding time step (t), but the candidate rejected the mutant; the middle 4 with cases where the candidate accepted the mutant, but the mutant rejected the candidate; and the last 4 with cases of mutual rejection. All 3 scenarios lead to the mutant remaining unmated at the start of time step $t + 1$.

Analogously to Equation A4, the probability the mutant has quality q^* and number of acceptances x^* at the start of time step $t + 1$ and is mated to a partner of quality q' is given by

$$
\begin{aligned}
p(t+1,q^*,x^*,q') = {} & p(t,q^*,x^*,q') \\
& + \varepsilon(a^*,q')\cdot\varepsilon(a,q^*) \sum_{q^*<a(t,x')} \sum_{q'<a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot\varepsilon(a,q^*) \sum_{q^*<a(t,x')} \sum_{q'\geq a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + \varepsilon(a^*,q')\cdot(1-\varepsilon(a,q^*)) \sum_{q^*\geq a(t,x')} \sum_{q'<a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x') \\
& + (1-\varepsilon(a^*,q'))\cdot(1-\varepsilon(a,q^*)) \sum_{q^*\geq a(t,x')} \sum_{q'\geq a^*(t,x^*-1)} p_{\text{meet}}(t,q^*,x^*-1,q',x').
\end{aligned}
\tag{B3}
$$

The first term gives the chance that the mutant had found a mate prior to time step t, whereas the last 4 give the chance that it found a mate in time step t.

Equations B1–B3 enable us to work out the probabilities that the mutant is in each possible state (i.e., each combination of q^*, x^*, and q') at $t = 2$ from the initial probability distribution at $t = 1$. We then repeat the process to obtain the same probabilities at $t = 3$, and so on until $t = T - 1$, when the mutant is assumed to accept its current candidate without error. The probability of being mated to an individual of quality q' in the final time step ($t = T$) is therefore

$$
\begin{aligned}
p(T,q^*,x^*,q') = {} & p(T-1,q^*,x^*,q') \\
& + \sum_{x'=0}^{T-2} p_{\text{meet}}(T-1,q^*,x^*,q',x')
\end{aligned}
\tag{B4}
$$

and $p(T, q^*, x^*, 0) = 0$ for all q^* and x^*.

Finally, using the probabilities obtained in Equations B3 and B4, we can calculate the total probability p_{mate} that the mutant mates with a partner of quality q' in any given time step t. We do this by taking the probabilities that the mutant mates by that time step and summing them over all qualities (q^*) and experiences (x^*) and then subtracting the chance that it had already mated in an earlier time step:

$$p_{\mathrm{mate}}(t,q') = \sum_{q^*=1}^{q_{\max}} \left(\sum_{x^*=1}^{t-1} p(t,q^*,x^*,q') - \sum_{x^*=1}^{t-2} p(t-1,q^*,x^*,q') \right). \tag{B5}$$

It is these p_{mate} probabilities that are used to calculate the expected fitness of the mutant (see main text).

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