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The tactics of mutual mate choice and competitive search

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Abstract A model of mutual mate choice is described, formulated as a dynamic game, which yields predictions about mating behaviour under the influence of time constraints, choice costs and competition for mates. These variables were examined because they may result in a change in the distribution of qualities among unmated individuals of both sexes over the course of the breeding season. The model predicts that mutual choice gives rise to assortative mating, although high costs of choice and/or inaccurate assessment both lead to lower overall correlations between the qualities (or the attractiveness) of mates. When all individuals are present from the start of the breeding season, the correlation between the qualities of individuals pairing at a given time declines throughout the season, so that mates are more closely matched among individuals who pair early than among those who pair late (and extra-pair copulation may thus be more common among the latter). Delayed arrival of lower-quality individuals may, however, lead to an increase in this correlation with time during the early part of the season. The mean quality of unmated males and females declines over time, because more attractive individuals tend to mate sooner. As a result of this decline, and because of time constraints, superior individuals become less choosy as the season progresses. If choice is costly, however, then inferior individuals become more selective with time during the early part of the season, and the level of choosiness peaks later for such individuals.

Key words Mate choice · Sexual selection · Search behaviour · Dynamic game

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Introduction

Animals of most species do not mate indiscriminately, but prefer some partners over others (Harvey and Bradbury 1991; Kirkpatrick and Ryan 1991; Wiley 1991; Ryan and Keddy-Hector 1992; Andersson 1994; Johnstone 1995). The origin and maintenance of such preferences, and their consequences for the evolution of sexual display, have been the subject of extensive theoretical and empirical research (reviewed by Andersson 1994). Only recently, however, have studies of mate choice begun to consider the ways in which individuals actually implement their preferences by sampling and selecting among potential partners. There is now growing evidence that in many species, individuals must assess mates sequentially rather than simultaneously, but are nevertheless able to choose more attractive partners (e.g. Gronell 1989; Trail and Adams 1989; Dale et al. 1990; Bensch and Hasselquist 1992; Petrie and Hunter 1993).

Theoretical analyses of various sequential sampling tactics suggest that when choice is costly, the optimal tactic is to accept males who exceed some critical level of quality, this level being adjusted to the expected return from continued search (Real 1990). Such models yield a number of testable predictions. When sampling is restricted to a finite time, for example, individuals should become less choosy as search progresses, while at any given time, they should be more choosy when search costs are lower and/or mates are more variable in quality (Real 1990). Empirical studies of sequential choice have since found evidence for a number of these effects (e.g. Alatalo et al. 1988; Bakker and Milinski 1991; Milinski and Bakker 1992; Palokangas et al. 1992).

Most existing models, however, have focused on single-sex discrimination, treating mate choice as an optimisation problem for either males or females alone (e.g. Janetos 1980; Real 1990; Dombrovsky and Perrin 1994; Getty 1995). This overlooks the potential for each sex to constrain choices by the other. When both sexes can exercise choice, a game theoretical approach must be used instead of simple optimisation, because the best strategy for males depends on the behaviour of females, and vice versa (Parker 1983; McNamara and Collins 1990; Crowley et al. 1991; Johnstone et al. 1996). For species such as the crested auklet, *Aethia cristatella*, in which there is evidence for both male and female choice (Jones and Hunter 1993), models of single sex discrimination are potentially misleading.

In addition to the above drawback, previous analyses have largely ignored the effects of competition on choice. Over the course of a breeding season, as mating takes place, the availability of potential partners may change, together with the distribution of qualities among unmated individuals. The optimal choice strategy will therefore change accordingly (Collins and McNamara 1993). It may be possible to overlook competition when considering female choice in non-resource-based mating systems such as leks, because males in these cases can mate with many different females without losing their value as partners (though sperm depletion might result in a decline in male mate value with repeated mating even under these circumstances Birkhead 1991; Birkhead et al. 1995). In resource-based mating systems, however, where theory predicts that mutual choice will be most common (see Johnstone et al. 1996), there is evidence that competition does restrict the opportunity for sampling mates (Dale et al. 1992). Mate choice under these circumstances represents a type of biological market (Noë and Hammerstein 1994, 1995)

Here, I present a model of mutual mate choice, formulated as a dynamic game, which takes into account the influence of time constraints, choice costs and competition for mates on mating behaviour. I then summarise the predictions of the model regarding individual sampling behaviour and the overall pattern of mating in a population exhibiting mutual choice. I conclude with a general discussion and a comparison between the present analysis and previous models of adaptive search.

An ESS model of mutual mate choice with competition

The model considers mate choice in a large, stable population of 1:1 sex ratio. Individuals of both sexes vary in quality, i.e. in their value as a mating partner to members of the opposite sex. Quality, denoted q, adopts discrete values evenly spaced between 0 and 1. The function $f(q)$ specifies the probability distribution of these values among individuals of each sex (the distributions of male and female qualities are assumed to be identical). Here, $f(q)$ is based on the quartic distribution shown in Fig. 1, with 20 possible levels of quality, but qualitatively similar solutions have also been obtained using other functions.

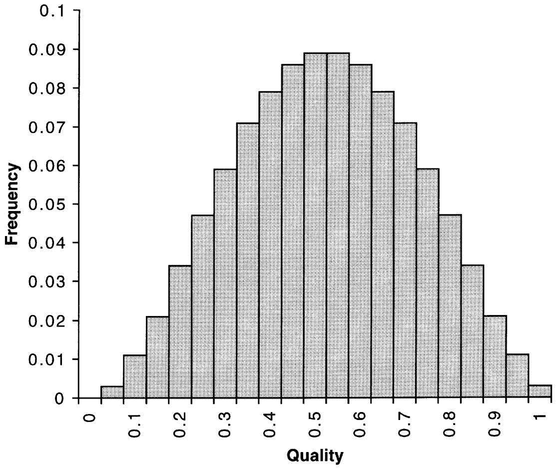

Fig. 1 Probability distribution of qualities, $f(q)$, among males and females in the population (there are 20 possible levels of quality)

Choice is restricted to a breeding season of finite length, divided into T discrete time steps (here $T = 15$). The temporal pattern in which individuals arrive at the breeding site, or otherwise become available for mating, is defined by the function $a(q,t)$, which specifies the probability that an individual (of either sex) of quality q arrives at the start of time step t (the distributions of male and female arrival times are assumed to be identical). The simplest case,

$a(q,t) = 1$ when $t = 1$, and
$a(q,t) = 0$ when $t \neq 1$

occurs when individuals "arrive" at the start of time step 1, and the whole breeding population is present from the very beginning of the season.

During each step, individuals that have arrived but not yet mated (initially, in the simplest case, the whole breeding population) pair up at random. Each member of a pair then makes an independent decision as to whether or not it will accept its current partner. Mating occurs if and only if both members of a pair choose to accept each other; forced copulation is not possible. Once mated, individuals "drop out" of the breeding pool, and are not subsequently available for pairing. During the last time step, all unmated individuals are assumed to accept their current partner, since there can be no further opportunity for sampling. There is no recall of previously encountered partners.

The fitness gain from mating (for individuals of either sex) is equal to the quality of the mating partner obtained. Sampling a new potential partner, i.e. engaging in a new round of random pairing and choice, entails a fitness cost c (the magnitude of which does not change over the course of the season).

A "choice strategy" specifies, for each quality of individual and for each time step, the probability that a potential partner of each possible quality will be accepted. At equilibrium, given that both sexes are assumed to share the same distribution of qualities and arrival times and the same costs of choice (and the sex ratio is 1:1), males and females will adopt the same choice strategy, denoted $p_{eq}(q,t,q')$. Note that this strategy does not incorporate learning; the overall distribution of qualities, $f(q)$, is assumed to be known from the beginning of the season, so that the probability of acceptance does not depend on the quality of previously encountered partners.

Calculating the equilibrium strategy

For any particular set of parameter values, the equilibrium strategy was found using a modification of the iterative best-response approach used by Johnstone (1994, 1996) to calculate evolutionarily stable strategies.

First, a candidate choice strategy, denoted $p_0(q,t,q')$, was chosen. The methods outlined in Appendix A were then used to calculate the probability distribution of qualities among unmated individuals at each time step, given that all members of the population adopt the strategy p_0. Having obtained the distribution of qualities for each time step, the methods outlined in Appendix B were used to construct a "best response" strategy, $p_{0\mathrm{r}}(q,t,q')$, described in more detail below. Together with the initial candidate strategy, this was then used to calculate a new choice strategy $p_1(q,t,q')$ defined by

$$p_1(q,t,q') = (1-\lambda)p_0(q,t,q') + \lambda p_{0\mathrm{r}}(q,t,q') \qquad (1)$$

(p_1 represents a strategy "intermediate" between the initial candidate strategy and its best response). The same process was then repeated, starting with p_1, to obtain a new strategy p_2, and so on.

Iteration was continued until the sequence of strategies p_1, p_2, p_3... and the sequence of best responses $p_{1\mathrm{r}}$, $p_{2\mathrm{r}}$, $p_{3\mathrm{r}}$... converged on a solution; that is, until a strategy was obtained that differed from its "best response" by no more than 0.00001 in any of the acceptance probabilities specified. The value of λ in Eq. 1, while always less than 1, was adjusted to facilitate rapid convergence. The value of λ was increased if the sequence of strategies exhibited directional convergence, and reduced if it exhibited oscillation.

The calculation of "best response" strategies, described in Appendix B, requires some explanation, because it incorporates the possibility of errors in choice (as suggested by J. McNamara, personal communication). An error-free best response would specify an acceptance probability of 1 when the expected fitness gain from accepting exceeds that from rejecting a potential partner, and an acceptance probability of 0 when the reverse is true. By contrast, the error-prone response strategies of the solution procedure were assumed to specify acceptance probabilities (for each possible combination of quality, time and partner quality) given by

$$p(q,t,q') = \frac{1+\tanh\left\{\frac{1}{k}\left[w_{\mathrm{accept}}(q,t,q') - w_{\mathrm{reject}}(q,t,q')\right]\right\}}{2} \qquad (2)$$

where $w_{accept}(q,t,q')$ and $w_{reject}(q,t,q')$ denote the expected fitness gained by accepting and by rejecting a potential mating partner, and k is a positive constant.

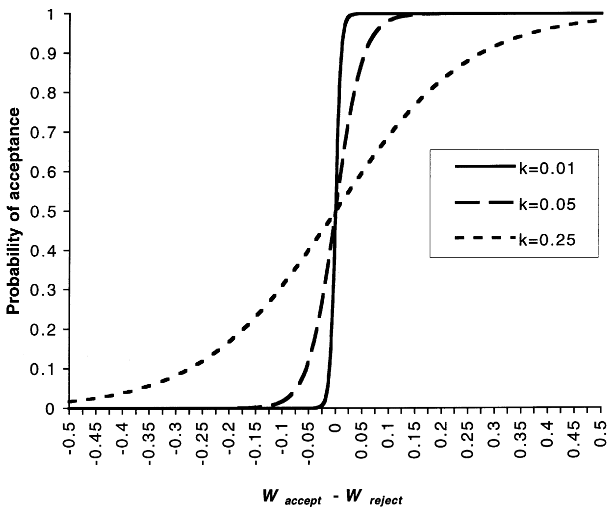

Fig. 2 Probability that a potential partner will be accepted, as a function of the expected fitness gain from acceptance relative to that from rejection, for three different values of k. Lower values of k indicate lower levels of error, and hence a closer approximation to the error-free best response strategy

Equation 2 implies that an individual is more likely to accept than to reject a partner when the fitness gained by accepting exceeds that gained by rejecting (and vice versa) but that there is an element of chance in the decision. The smaller the benefit to be gained by accepting (or rejecting), the less certain it is that this option will be chosen; in the extreme, when acceptance and rejection yield equal payoffs, both are equally likely (see Fig. 2). This type of response is similar to that obtained by explicitly incorporating perceptual error in a choice model (Getty 1995; Johnstone 1996). The constant k determines the degree of error, or in other words, how sensitive individuals are to small differences in mate value. For low values of k, the response strategy specified by Eq. 2 closely approximates the error-free best response. For higher values of k, however, the approximation becomes less and less accurate, as the sharp acceptance threshold specified by the error-free strategy is increasingly blurred (see Fig. 2).

Once an equilibrium strategy was obtained, forward simulation (see Mangel and Clark 1988) could be used to determine the expected pattern of mating in a population adopting that strategy. Aspects of mating patterns calculated in this way, for various different parameter values, are presented in the next section.

Results

Figure 3a summarises a sample equilibrium choice strategy, for the case in which $c = 0.02$, $k = 0.01$ and all members of the breeding population are present from the start of the season. The graph shows, for each time step, the threshold mating value above which a potential partner will be accepted with a probability of at least 0.5 by individuals of four representative qualities, $q = 0.15$,

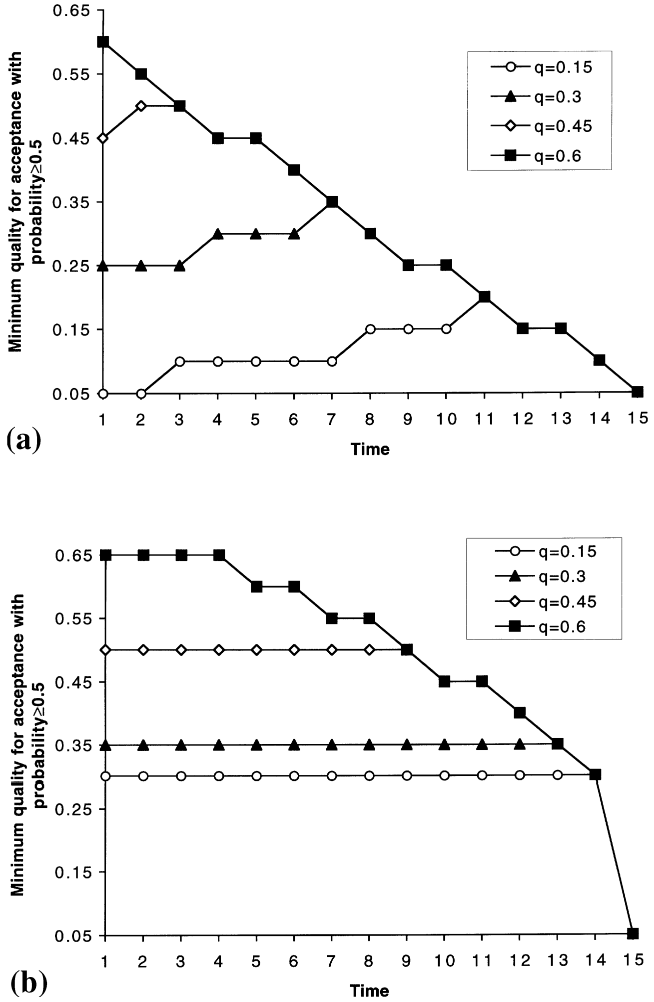

Fig. 3a, b The threshold mating value above which a potential partner will be accepted with a probability of at least 0.5, as a function of time, by individuals of four representative qualities ($q = 0.15$, $q = 0.3$, $q = 0.45$, $q = 0.6$), when $k = 0.01$ and all members of the breeding population are present from the start of the season. The cost of choice for the strategy shown in graph **a** is $c = 0.02$, while for graph **b** it is $c = 0$ (implying cost-free sampling)

$q = 0.3$, $q = 0.45$ and $q = 0.6$. All individuals whose quality is greater than or equal to 0.6 exhibit the same level of choosiness. For high quality individuals (in this case for those with $q \geq 0.55$), the threshold declines continuously over the course of the breeding season, reaching the minimum possible value in the final time step. In other words, such individuals become less choosy as the season progresses. By contrast, the acceptance threshold of poor-quality individuals, which is lower than that of high quality mates, increases over the early part of the season. Eventually, it peaks and begins to decline, but it does so at successively later times for individuals of decreasing quality. Figure 3b, which shows a similar graph for the case in which $c = 0$ (and $k = 0.01$), reveals that this initial increase in choosiness is a consequence of the costs of choice. When sampling incurs no direct costs, the acceptance thresholds of all individuals decline with time.

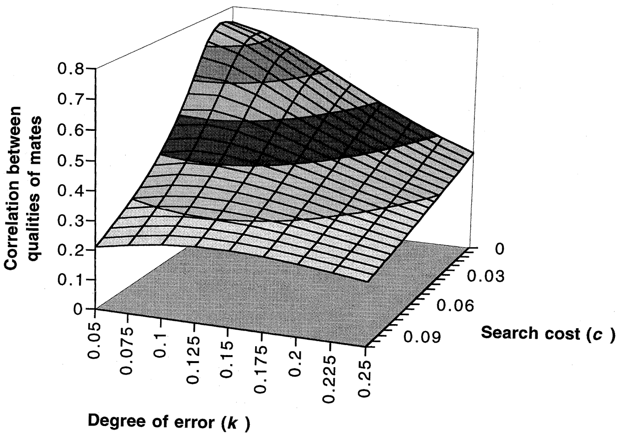

Fig. 4 Overall correlation between the qualities of mates, as a function of c, the cost of choice, and k, the degree of error

Stable choice strategies such as those illustrated in Fig. 3 give rise to assortative mating, so that high-quality individuals tend to acquire high-quality partners. Figure 4 shows the overall correlation between the qualities of male and female partners (calculated at the end of the season, when all individuals have paired), as a function of c, the cost of sampling, and k, the degree of error. As the graph shows, low costs and low levels of error favour closely assortative pairing, while high costs and/or a high degree of error tend to result in lower correlations between the qualities of partners. One exception to this general trend is that at low levels of error, the correlation decreases slightly as search costs approach zero.

Assortative mating implies that high quality individuals acquire high quality mates. The model predicts that they will also acquire partners earlier. Figure 5 presents the mean time to mating (a value of 1 denoting the first time step, and one of 15 the last) as a function of quality, for four different values of c in Fig. 5a, and for four different values of k in Fig. 5b. In all cases, superior individuals tend to mate sooner. Choosiness increases with quality up to a point, but levels off above $q = 0.55$ (as mentioned above, all individuals with $q \geq 0.6$ adopt the same choice strategy). Consequently, superior individuals are acceptable to wider range of partners, while being no more likely to reject potential mates themselves, which results in more rapid pairing. The figure also reveals that higher costs of choice lead to more rapid mating by all individuals, while the degree of error has little overall effect on time to pairing.

As a result of early pairing by superior males and females, the mean quality of unmated individuals (of either sex) declines over the course of the breeding season, as shown in Fig. 6. Increased search costs lead to more rapid pairing, which results in a steeper decline in the quality of unmated individuals. The degree of error, by contrast, has little effect.

Figure 7 shows the correlation between the qualities of individuals pairing during each time step, for four

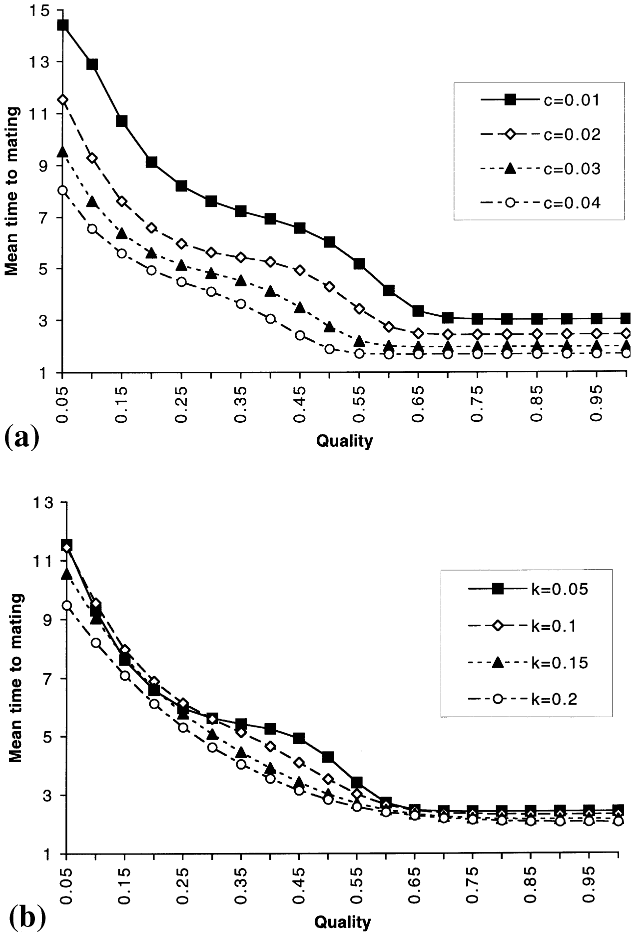

Fig. 5a, b Mean time to mating (a value of 1 indicating denoting the first time step, and one of 15 the last) as a function of quality, when all members of the breeding population are present from the start of the season. Graph **a** shows results for four different values of *c*, the cost of choice ($c = 0.01$, $c = 0.02$, $c = 0.03$ and $c = 0.04$), with $k = 0.05$, while graph **b** shows results for four different values of *k*, the degree of error ($k = 0.05$, $k = 0.1$, $k = 0.15$ and $k = 0.2$), with $c = 0.02$

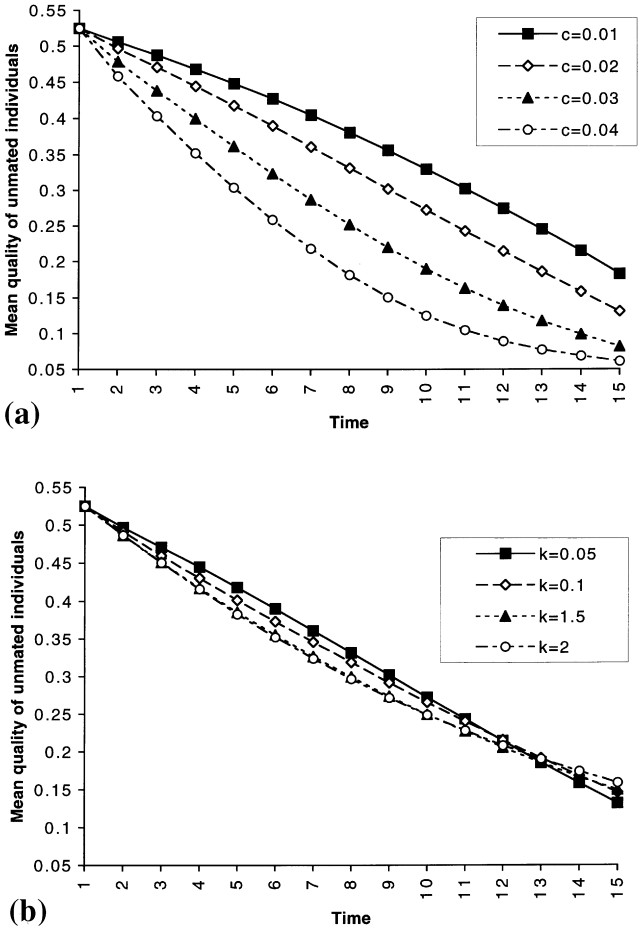

Fig. 6a, b Mean quality of unmated individuals as a function of time, when all members of the breeding population are present from the start of the season. Graph **a** shows results for four different values of *c*, the cost of choice ($c = 0.01$, $c = 0.02$, $c = 0.03$ and $c = 0.04$), with $k = 0.05$, while graph **b** shows results for four different values of *k*, the degree of error ($k = 0.05$, $k = 0.1$, $k = 0.15$ and $k = 0.2$), with $c = 0.02$

different values of *c* in Fig. 7a, and for four different values of *k* in Fig. 7b. As previously mentioned, lower sampling costs and lower levels of error generally lead to higher correlations (although at low levels of error, the correlations start to decrease as search costs approach zero). The figure also reveals that for given levels of cost and of error, the correlation declines over time. Among individuals pairing early, in other words, high quality males tend to mate with high quality females, and low quality males with low quality females. Among those pairing late, by contrast, mating is more random.

Finally, Fig. 8 illustrates the way in which the pattern of individual arrival at the breeding site can influence mating. The results presented in the graph were generated using arrival functions (which specify the probability that an individual of quality *q* arrives during time step *t*) of the form

$$a(q,t) = \frac{t!}{t!(T-t)!}\left[d(1-q)\right]^{t}\left[1-d(1-q)\right]^{T-t}$$

In other words, arrival times were assumed to follow a binomial distribution for individuals of each quality, with lower-quality individuals tending to arrive later. The parameter *d* determines the spread of arrival times. When $d = 0$, all individuals are present from the start of the season; as *d* increases, the arrival of lower-quality males and females is increasingly delayed relative to that of the best individuals.

Figure 8 presents the correlation between the qualities of mates pairing during each time step for four different values of *d*. The graph reveals that as arrival times become more spread out, the correlation during the early part of the breeding season drops. It should be noted, however, that this does not entail a significant decrease in the overall correlation between the qualities of mates calculated at the end of the season (when all individuals have paired), which varies by less than 5% over the range of arrival patterns considered. When *d* is large, most individuals present during the early part of the season are of high quality, so that random (or only

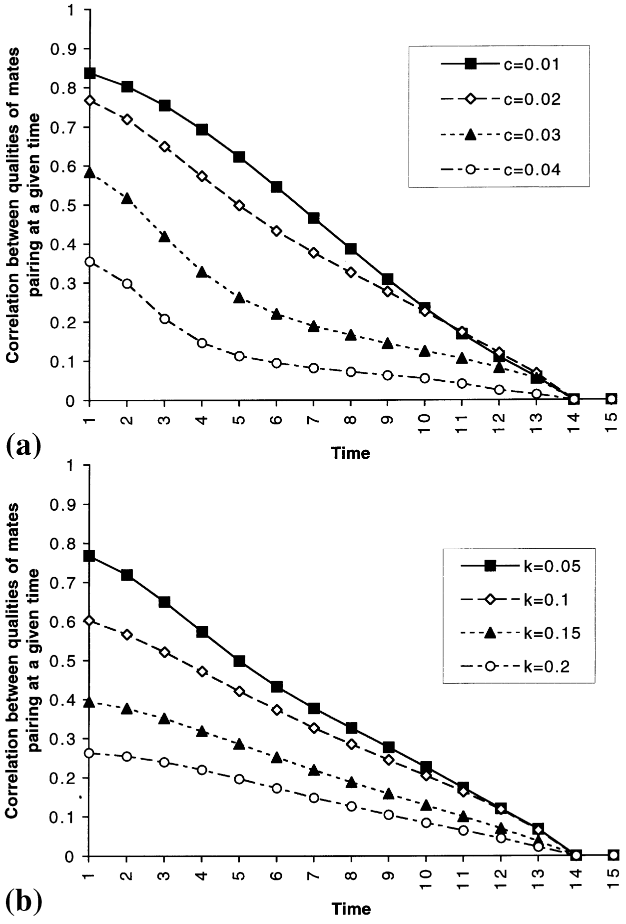

Fig. 7a, b Correlation between the qualities of individuals pairing at different times, when all members of the breeding population are present from the start of the season. Graph **a** shows results for four different values of *c*, the cost of choice ($c = 0.01$, $c = 0.02$, $c = 0.03$ and $c = 0.04$), with $k = 0.05$, while graph **b** shows results for four different values of *k*, the degree of error ($k = 0.05$, $k = 0.1$, $k = 0.15$ and $k = 0.2$), with $c = 0.02$

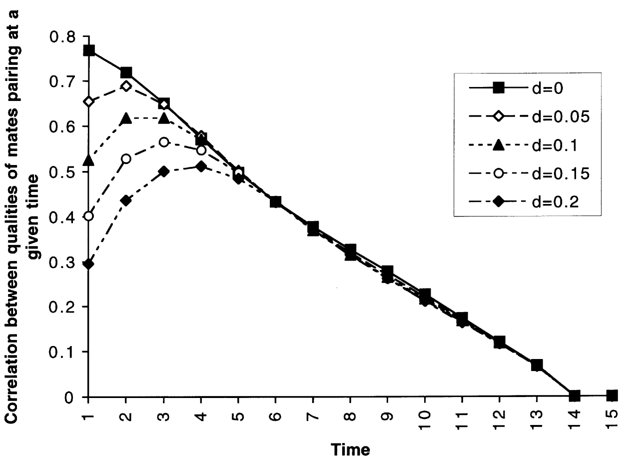

Fig. 8 Correlation between the qualities of individuals pairing at different times, for different patterns of individual arrival at the breeding site. The graph shows results for four different values of *d*, which determines the degree to which lower-quality males and females are delayed in their arrival. The degree of error was in all cases $k = 0.05$, and the cost of choice $c = 0.02$

coarsely assortative) pairing during this period does not disrupt the overall correlation.

Discussion

Stable sampling strategies

The model predicts that high quality individuals should become less choosy as the season progresses. This matches the predictions of models of single-sex discrimination (Real 1990; Collins and McNamara 1993), and is readily explicable in terms of time constraints and the effects of competition. As the end of the season approaches, fewer opportunities for sampling remain, and the expected future fitness gains from continuing to search for a mate are consequently lower. Moreover, since high-quality individuals more rapidly find a partner and drop out of the mating pool than do low-quality individuals, the mean quality of unmated individuals declines as the season progresses. Both of these effects favour lower levels of choosiness later on.

More surprisingly, the model suggests that when choice is costly, low-quality individuals are likely to become more choosy with time, at least during the early part of the season. How can this early increase in choosiness be explained, given the effects of time constraint and competition? Poor-quality individuals have little hope of being accepted by a valuable partner early in the season because (as described above) high-quality individuals can afford to be choosy at this time. Consequently, the expected future fitness that poor-quality individuals stand to gain from searching is low, and they will accept an inferior mate. As time passes, the mean quality of unmated individuals may drop, but so does their level of choosiness. Because of time constraints, high-quality individuals can no longer afford to reject low-quality partners, so that even inferior individuals have a chance of acquiring a valuable mate. The expected future fitness that poor-quality individuals stand to gain rises accordingly, and so does their acceptance threshold (given the chance of acquiring a valuable partner in the near future, it pays to reject a low-quality mate that might have been acceptable earlier in the season). Once the point is reached where a low-quality individual becomes acceptable to all potential partners, however, the motive for this increase in choosiness is lost, and the acceptance threshold begins to decline again. This point comes at a later stage of the breeding season for lower-quality individuals simply because stronger time constraints are needed to render them acceptable to superior mates.

The initial increase in choosiness is of low-quality individuals is lost, however, when sampling incurs no direct costs (i.e. when $c = 0$; Fig. 3b). Under these circumstances, a low quality-individual can always afford to wait until the point where he or she becomes acceptable to higher-quality partners, so that it pays to reject a potential mate of low value even in the early part of the season. Consequently, when there are no costs of choice, there is no increase in choosiness with time.

Patterns of mating

The present model, like earlier analyses of dual-sex choice (Burley 1983; Parker 1983; McNamara and Collins 1990; Johnstone et al. 1996), suggests that mutual choice will give rise to assortative mating. High quality males and high quality females will tend to pair together, as will low quality males and low quality females (though individuals above some threshold quality will prove acceptable to all partners at all times). Moreover, in line with the findings of Johnstone et al. (1996), the degree of positive assortment is predicted to depend on the magnitude of search costs, with low costs favouring accurate assortment. Unsurprisingly, the degree of error is also predicted to exert a similar influence, with low error favouring closely assortative mating.

The model further allows one to consider how the pattern of mating changes over time. The most robust prediction is that the mean quality of unmated individuals should decline over time, because superior individuals tend to find a mate more quickly. Concomitantly, the mean quality of individuals pairing early in the season should be higher than that of late pairing individuals, even when arrival time is not related to quality (though earlier arrival of superior individuals should enhance this pattern).

When all individuals are present from the start of the breeding season, the model also predicts that the correlation between individuals pairing at a given time should decrease as the season progresses. This is a consequence of the decline in choosiness (particularly among high-quality individuals) discussed above. Late in the season, time constraints and the drop in mean quality of unmated individuals lead to lower acceptance thresholds for males and females, so that mating becomes more random. The trend is, however, sensitive to the pattern of arrival at the breeding site (i.e. the times at which individuals of different qualities become available for mating). Delayed arrival of low-quality individuals leads to lower correlations between the qualities of mates pairing during the early part of the breeding season. This occurs because most of the mates present are then of sufficient value that all are acceptable to one another. Only when low-quality individuals start to arrive in substantial numbers does choice become necessary, yielding higher correlations. As pointed out in the results section, however, delayed arrival of low-quality mates does not lower the overall correlation (calculated at the end of the season) between the qualities of partners, because random mating among the high-quality individuals present at the start of the season still yields positive assortative mating overall.

Since mismatches in partner attractiveness are likely to promote extra-pair copulation (EPC), with the more attractive member of a pair seeking to locate superior mates (Petrie and Hunter 1993), the above pattern may lead to increased frequencies of EPCs among late-pairing individuals. The time available for mate choice, as well as the cost of sampling, is thus likely to exert a considerable influence on the mating system of a species, with strong time constraints favouring more extra-pair activity.

Comparison with previous models

Few previous models have addressed the issue of mutual mate choice. Parker (1983) was the first to point out the need for a game-theoretic treatment of this topic, but did not attempt a rigorous analytical solution of the problem. McNamara and Collins (1990) later obtained such a solution, and Johnstone et al. (1996), by relating the sex-specific costs and benefits of choice to biologically meaningful parameters, were able to use a similar approach to explain sex and species differences in mate choice. These studies, however, adopted an infinite horizon rate-maximisation approach, calculating stable choice strategies for a population in which individuals alternate continuously between searching for partners and "processing" the matings thus acquired. Consequently, they cannot yield predictions about the behaviour of males and females who have only a limited time in which to find a mate.

The incorporation of time constraints in the present model does not alter its predictions about the broad pattern of mating (see above). It does, however, lead to very different predictions regarding individual sampling and choice behaviour. The above studies suggested that mutual choice would give rise to broadly assortative mating overlying random choice within sequential subranges of quality (McNamara and Collins 1990; Johnstone et al. 1996). By contrast, the present model predicts that individual acceptance thresholds will vary continuously with quality (up to a point — mates whose quality exceeds some critical level still prove universally acceptable).

The only previous study to have considered mutual choice during a finite breeding season is that of Crowley et al. (1991). Their model incorporates just two quality groups in each sex, and it does not yield detailed predictions regarding the pattern of mating. However, one clear result was that, when mate density remains constant throughout the breeding season, choosiness should increase with time. This contrasts with the results of the present model, which predicts a drop in choosiness (at least for high-quality individuals, or low-quality individuals late in the season) even though encounter rate is assumed to remain constant. There are two reasons for this difference. First, Crowley et al. (1991) did not consider the effects of competition, but assumed that individuals could mate many times, so that the frequency of low- and high-quality males and females did not change as a result of mating. Second, they assumed that choice costs took the form of increased predation risk that jeopardised future reproduction during the mating season. Because there was no potential contribution to fitness from reproduction in future years, effective costs decreased towards the end of the season, as there was then less potential future reproduction to jeopardise.

Future modelling possibilities

The present model makes a number of simplifying assumptions, thus leaving considerable scope for further analyses of mutual mate choice. The most obvious topic that remains to be dealt with is that of sex differences in choosiness. Because males and females are assumed to share the same distribution of qualities and arrival times and the same costs of choice, and because the sex ratio is 1:1, the present model yields a single equilibrium choice strategy for individuals of either sex. In reality, however, the operational sex ratio may often deviate from equality, and one sex may often arrive at the breeding site later than the other, or find choice more costly. All of these factors are likely to favour sex differences in choosiness, and thus give rise to distinct male and female choice strategies (see Johnstone et al. 1996). The modelling framework described above can (with some modification) readily accommodate sex-specific choice behaviour, and analysis of an extended version of the present model that incorporates sex differences is currently underway (Johstone in prep.).

A second issue that remains to be addressed is the role of learning in mutual choice. While most existing models of mate choice (including the present one) have assumed that the distribution of qualities among potential partners is known from the start of the breeding season (e.g. Janetos 1980; Real 1990; McNamara and Collins 1990; Crowley et al. 1991; Collins and McNamara 1993; Johnstone et al. 1996), this is unlikely to be the case. Both mean quality and the degree of variation in mate value are likely to change from one breeding season to the next, so that individuals may need to sample several potential partners in order to estimate the current distribution (see Dombrovsky and Perrin 1994). No attempt has yet been made to assess the impact of such uncertainty in the context of mutual choice.

Thirdly, the model assumes that search costs do not change over the course of the breeding season. This implies that unmated individuals can continue to locate each other with relative ease, even late in the season when many males and females have already paired. For some species, however, the costs of choice may increase with time, due to a decline in the density of potential partners. Incorporation of increasing costs is unlikely to alter qualitatively the conclusions of the model, but would favour a more rapid drop in choosiness with time (among individuals of all qualities).

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Appendix A

Calculation of the population consequences of a choice strategy

Let $f_t(q)$ denote the distribution of qualities among unmated individuals (of either sex) at the start of time step t, and $m_t(q)$ the proportion of individuals of quality q (of either sex) who have arrived but have not yet mated at that time. Initially, the pool of unmated individuals comprises all those who have arrived, so that

$$m_1(q) = a(q,1)$$

and

$$f_1(q) = \frac{f(q)m_1(q)}{\sum_x f(x)m_1(x)}$$

where $f(Q)$ is the probability distribution of qualities in the breeding population as a whole (as shown in Fig. 2), and $a(q,t)$ is the function specifying the temporal pattern of arrival. The distribution of qualities during later time steps can be obtained by repeated evaluation of the following equations:

$$m_{t+1}(q) = m_t(q)\left[1 - \sum_{q'} f_1(q')p(q,t,q')p(q',t,q)\right] + a(q,t+1)$$

$$f_{t+1}(q) = \frac{m_{t+1}(q)f(q)}{\sum_x m_{t+1}(x)f(x)}$$

where $p(q,t,q')$ is the choice strategy adopted by individuals in the population. The right-hand term inside the brackets in the first expression represents the proportion of unmated individuals of quality q, present at the breeding site, who mate during time step t. This value is obtained by summing, over all possible partner qualities, the probability of encountering, accepting and being accepted by a partner of that quality.

Appendix B

Calculation of an error-prone "best response" strategy

Let $w(q,t,q')$ denote the expected future fitness gain of an individual (of either sex) of quality q who, having previously encountered and rejected $t-1$ potential mates, has just been paired (during time step t) with a partner of quality q'. Given that the breeding season lasts for only T time steps, we can easily determine $w(q,T,q')$, the expected future fitness gain of an individual who has just encountered its last possible partner, because the decision adopted by such an individual is always to mate (there being no further opportunity for sampling). This value is simply equal to q', the quality or mating value of the partner. At earlier stages of the breeding season, acceptance probability is given by

$$p(q,t,q') = \frac{1 + \tan h\{\frac{1}{k}[w_{\text{accept}}(q,t,q') - w_{\text{reject}}(q,t,q')]\}}{2}$$

and expected future fitness gain by

$$w(q,t,q') = p(q,t,q')w_{\text{accept}} + [1 - p(q,t,q')]w_{\text{reject}}$$

where

$$w_{\text{accept}}(q,t,q') = q'$$

and

$$w_{\text{reject}}(q,t,q') = \sum\nolimits_x f_{t+1}(x)w(q,t+1,x) - c$$

Backwards iteration of the above equations, starting from time step $T{-}1$, yields expected future fitness gain and acceptance probability for each possible pair of values q and q' at successively earlier time steps, until the beginning of the breeding season is reached.

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