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Optimal assessment of multiple cues

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In a wide range of contexts from mate choice to foraging, animals are required to discriminate between alternative options on the basis of multiple cues. How should they best assess such complex multicomponent stimuli? Here, we construct a model to investigate this problem, focusing on a simple case where a 'chooser' faces a discrimination task involving two cues. These cues vary in their accuracy and in how costly they are to assess. As an example, we consider a mate-choice situation where females choose between males of differing quality. Our model predicts the following: (i) females should become less choosy as the cost of finding new males increases; (ii) females should prioritize cues differently depending on how choosy they are; (iii) females may sometimes prioritize less accurate cues; and (iv) which cues are most important depends on the abundance of desirable mates. These predictions are testable in mate-choice experiments where the costs of choice can be manipulated. Our findings are applicable to other discrimination tasks besides mate choice, for example a predator's choice between palatable and unpalatable prey, or an altruist's choice between kin and non-kin.

Keywords: multiple cues; mate choice; sequential sampling; discrimination task

1. INTRODUCTION

It is increasingly apparent that animal displays frequently consist of multiple cues (Jennions & Petrie 1997). There may be simple psychological reasons for this: data from humans and other animals suggest that multiple stimuli are more effective in eliciting a response than a single stimulus (Rowe 1999). A growing number of empirical studies have demonstrated that multiple cues in sexual displays have an important influence on mate choice (e.g. Dale & Slagsvold 1996; Hill *et al.* 1999; Kodric-Brown & Nicoletto 2001). Previous theoretical work has shown how preferences for multiple ornaments can arise (e.g. Iwasa & Pomiankowski 1994; Johnstone 1996), but little attention has focused on the precise nature of these preferences: given that males possess multiple cues, how should females best assess them?

To investigate this problem, we constructed a general model analogous to the job-search models developed by economists (Lippman & McCall 1976). We imagine a simple situation where there are two types of male, 'desirable' and 'undesirable'. Females sample males sequentially, paying a cost to locate each successive male, and can discriminate between them using two cues, which may differ in their accuracy and in how costly they are to assess. At any point the female can terminate her search and mate with the current male. We calculate the expected pay-off of each of the possible strategies of female choice and identify which is favoured under various sets of conditions.

To make an adaptive mate-choice decision, females need to gather information about prospective mates efficiently (Gigerenzer & Todd 1999). Evidence from a wide range of species (reviewed by Andersson 1994) suggests that many cues subject to female choice convey information about the quality of the males possessing them (Zahavi 1975). In our model, we assume that these cues may differ in how accurately they reflect male quality and in the ease with which they can be assessed by females, as suggested by several authors (e.g. Sullivan 1994; Hill *et al.* 1999; Kodric-Brown & Nicoletto 2001).

Here, we investigate a discrimination task, where females must choose between two types of male. In nature, females may need to discriminate between conspecific and heterospecific males, or between sexually mature and juvenile males. Our model is best suited to this kind of scenario; however, it is also a useful first step towards modelling situations where there is continuous variation in male quality.

The general nature of our model makes it applicable to any discrimination task involving multiple cues. Three examples are: a predator's choice between palatable and unpalatable prey; a parent's choice between its own offspring and brood-parasitic young; and a worker ant's choice between fellow colony members and alien intruders. To aid understanding, we focus on a mate-choice scenario.

2. THE MODEL

(a) *Basic structure of the model*

We imagine a population containing two types of male, a 'desirable' type, at frequency f, and an 'undesirable' type, at frequency $1-f$ (where $0 \leqslant f \leqslant 1$). Females encounter males sequentially and at random and pay a sampling cost c for each male they meet, reflecting the time or effort spent locating them. On each encounter, a female chooses whether to terminate her search and mate with the current male, or to reject him and move on.

To help her reach her decision on a particular male, she can assess his display, examining the cues sequentially. For each cue i she examines she pays an assessment cost a_i, reflecting the time or energy spent on assessment. In most biological systems, this cost should be considerably smaller than the sampling cost c. To simplify matters, the

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male display consists of just two independent cues. These show all-or-nothing expression, though this may reflect some threshold level that the females are looking for in a continuously variable cue.

If cue i is perfectly accurate, all desirable males will express it whereas all undesirable males will lack it. However, in keeping with the error that exists in biological recognition systems, we envisage some probability e_i that desirable males are perceived to lack the cue and undesirable males are perceived to possess it. To keep our model simple, desirable males are perceived to lack the cue with the same probability that undesirable males are perceived to possess it: in the terminology of Reeve (1989), acceptance and rejection errors are symmetrical. Thus desirable males are perceived to express cue i ($i = 1, 2$) with probability $1 - e_i$ while undesirable males are perceived to do so with probability e_i, where $0 \leqslant e_i \leqslant 0.5$. When $e_i = 0$ the cue i shows perfect accuracy, but as e_i increases the cue becomes less accurate.

If a female decides to mate with a particular male, she does not mate again. If her chosen mate is of the desirable type, she receives an additive fitness pay-off, the 'benefit of discrimination'. For convenience this pay-off is set to one; thus the parameters c and a_i become the costs of sampling and assessment, respectively, relative to the pay-off from mating with a desirable male.

(b) *Female strategies*

How should a female use the multiple cues to pick a suitable mate? We consider seven possible strategies, beginning with the most choosy:

(i) both-one: accept only males with both cues; assess cue one first (assesses a second cue if the first is present);
(ii) both-two: accept only males with both cues; assess cue two first (assesses a second cue if the first is present).

Less choosy than this are strategies that require only one of the cues to be present:

(iii) one: accept only males with cue one (only assesses one cue);
(iv) two: accept only males with cue two (only assesses one cue).

Less choosy still are strategies that require only one cue, but do not care which:

(v) either-one: accept males with either cue; assess cue one first (assesses a second cue if the first is absent);
(vi) either-two: accept males with either cue; assess cue two first (assesses a second cue if the first is absent).

Finally, the least choosy females will accept a male regardless of his cues:

(vii) anyone: accept any male (never assesses any cues).

All of these strategies show sequential sampling, with females continuing to search until they meet a male that exceeds their acceptance threshold. They differ in the permissiveness of these thresholds. Other possible strategies exist in which males are rejected on the basis of possessing a given cue for example, the decision rule 'accept only males with cue one but not cue two'. However, because in our model desirable males are more likely than undesirable males to possess the cue, such strategies will always have lower fitness than one or more of the alternatives listed above.

(c) *Expected pay-offs*

A female playing the strategy 'anyone' pays a one-off sampling cost c to locate a male, and then ends her search and mates with him. With probability f he is of the desirable type, in which case she obtains the benefit of discrimination. Her expected pay-off, W_{anyone}, is therefore

$$W_{\text{anyone}} = -c + f. \tag{2.1}$$

A female playing 'either-one' pays a cost c to locate a male, and then a second cost a_1 to assess his cue one. She accepts him with probability P(cue one), the probability that a randomly encountered male possesses cue one, and in doing so ends her search and mates with him. The chance that she then gets the benefit of discrimination is given by P(desirable | cue one), the probability that a male is of the desirable type given that he possesses cue one. If, however, the male she meets lacks cue one (probability P(not cue one)), she will go on to assess the second cue, paying a cost a_2. She accepts him with probability P(cue two | not cue one) and will then gain the benefit of discrimination with probability P(desirable | cue two, not cue one). However, there is a probability P(not cue two | not cue one) that he also lacks cue two, in which case she will reject him and be in the same position she started in, with expected future fitness W. As an equation:

$$\begin{aligned} W = {} & -c - a_1 + P(\text{cue one}) \times P(\text{desirable} \mid \text{cue one}) \\ & + P(\text{not cue one}) \times (-a_2 + P(\text{cue two} \mid \text{not cue one}) \\ & \times P(\text{desirable} \mid \text{cue two, not cue one}) \\ & + P(\text{not cue two} \mid \text{not cue one}) \times W), \end{aligned}$$

which, after rewriting these probabilities in terms of f and e_i, becomes

$$\begin{aligned} W = {} & -c - a_1 + (f + e_1(1-2f))\frac{f(1-e_1)}{f + e_1(1-2f)} \\ & + (1 - f - e_1(1-2f)) \\ & \times \left(-a_2 + \frac{e_1 f - e_2(e_1 + f - 1)}{1 - f - e_1(1-2f)}\right. \\ & \times \frac{e_1(1-e_2)f}{e_1 f - e_2(e_1 + f - 1)} \\ & \left. + \left(1 - \frac{e_1 f - e_2(e_1 + f - 1)}{1 - f - e_1(1-2f)}\right) W\right). \end{aligned}$$

Solving for W, this gives the expected pay-off to 'either-one' as

$$W_{\text{either-one}} = \frac{-c - a_1 + f(1 - e_1 e_2) - a_2(1 - f - e_1(1-2f))}{f + e_2(1-f) + e_1(1-f) - e_1 e_2}. \tag{2.2}$$

Expected pay-offs of the other strategies are calculated in the same way and are as follows:

$$W_{\text{either-two}} = \frac{-c - a_2 + f(1 - e_1 e_2) - a_1(1 - f - e_2(1-2f))}{f + e_2(1-f) + e_1(1-f) - e_1 e_2}, \tag{2.3}$$

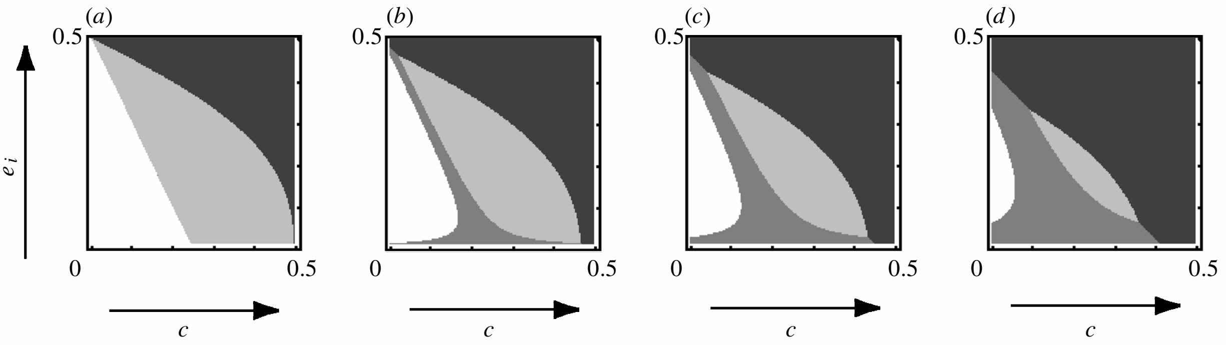

Figure 1. Optimal mate-assessment strategies for varying levels of sampling cost, c, and error in assessing cues, e_i. White areas, 'both'; light-grey areas, 'either'; mid-grey areas, 'one', 'two'; dark-grey areas, 'anyone'. The frequency of desirable males, f, is set at 0.5. The four plots show a sequence of increasing assessment cost: (*a*) $a_i = 0$; (*b*) $a_i = 0.01$; (*c*) $a_i = 0.02$; and (*d*) $a_i = 0.04$.

$$W_{\text{one}} = \frac{-c - a_1 + (1 - e_1)f}{e_1(1 - 2f) + f}, \tag{2.4}$$

$$W_{\text{two}} = \frac{-c - a_2 + (1 - e_2)f}{e_2(1 - 2f) + f}, \tag{2.5}$$

$$W_{\text{both-one}} = \frac{-c - a_1 + f(1 - e_1 - e_2 + e_1e_2) - a_2(f + e_1(1 - 2f))}{(1 - e_1)f - (f - e_1)e_2}, \tag{2.6}$$

$$W_{\text{both-two}} = \frac{-c - a_2 + f(1 - e_1 - e_2 + e_1e_2) - a_1(f + e_2(1 - 2f))}{(1 - e_1)f - (f - e_1)e_2}. \tag{2.7}$$

(d) *The optimal strategy*

By manipulating the parameter values and observing the effect on the pay-off functions, we can identify which strategy gives the biggest pay-off for given levels of cue accuracy, assessment cost, sampling cost and the frequency of desirable mates. A basic prediction is that it should pay females to favour cues that are accurate and cheap to assess. It is less clear what they should do when the most accurate cues are also those that are most costly to assess.

3. RESULTS

Unsurprisingly, the expected number of males a female samples before she accepts one increases with the choosiness of the strategy, from 'anyone' (least choosy) to 'both-one' and 'both-two' (most choosy). When desirable males are common (f high) the number sampled increases as the cues become less accurate, but when desirable males are rare (f low) the opposite happens. The highest number of males is sampled when desirable males are rare and cues are highly accurate.

(a) *Cues equally accurate* ($\mathbf{e}_1 = \mathbf{e}_2$) *and equally costly to assess* ($\mathbf{a}_1 = \mathbf{a}_2$)

The results for equal accuracies and equal assessment costs are summarized in figure 1. There is no difference in pay-off between the 'both' strategies ('both-one', 'both-two'), between the single-cue strategies ('one', 'two') or between the 'either' strategies ('either-one', 'either-two') as the two cues are effectively identical.

As the sampling cost c increases, less choosy strategies are favoured. When there is no cost of assessing traits ($a_1 = a_2 = 0$), the optimal strategy changes from 'both' to 'either' to 'anyone' as the sampling cost rises, reflecting a sequence of decreasing choosiness. Females that consider only a single cue ('one', 'two') are never favoured when the assessment cost is zero.

When a cost of assessment is introduced ($a_1 = a_2 > 0$), single-cue strategies ('one', 'two') can be favoured for intermediate values of the sampling cost. As the assessment cost is raised, the single-cue strategies are increasingly favoured and displace the multi-cue strategies of 'both' and 'either'. If the assessment cost is greater than $(e_i(1 - e_i)(1 - 2e_i))/((1 + 4e_i(1 - e_i))$, the 'both' and 'either' strategies are never favoured, whatever the sampling cost.

As cue accuracy decreases (increasing $e_1 = e_2$), less choosy strategies are favoured. If assessment costs are large and both cues are highly accurate, it can pay to use just one cue to assess males ('one', 'two') over a wide range of sampling costs.

Altering the frequency of desirable males also affects which strategies are favoured. When f is changed from 0.5 to 0.8 (desirable mates are common), the unselective 'anyone' strategy is optimal over a smaller region of the parameter space (only when search cost c and error e_i are high); when it is decreased to 0.2 (desirable mates are rare), 'anyone' is the only optimal strategy above a search cost of $c = 0.2$, however accurate the cues.

(b) *Cues differ in accuracy* ($\mathbf{e}_1 \neq \mathbf{e}_2$) *and in cost of assessment* ($\mathbf{a}_1 \neq \mathbf{a}_2$)

Figure 2 shows the effect of increasing sampling cost c on the strategies favoured for different combinations of cue accuracies e_1 and e_2, for $f = 0.2$ (we consider the effect of changing f below). Now, which cue is assessed first by the multi-cue strategies can affect their pay-off.

When the sampling cost is low, the choosy strategies 'both-one' and 'both-two' are optimal over the majority of the parameter space. As the sampling cost is increased, the choosy 'both' strategies are profitable only where both cues are highly accurate, and the less choosy strategies 'either-one' and 'either-two' are favoured over much of the parameter space. At these intermediate levels of the sampling cost, females paying attention to only one cue ('one', 'two') are favoured if that cue is considerably more

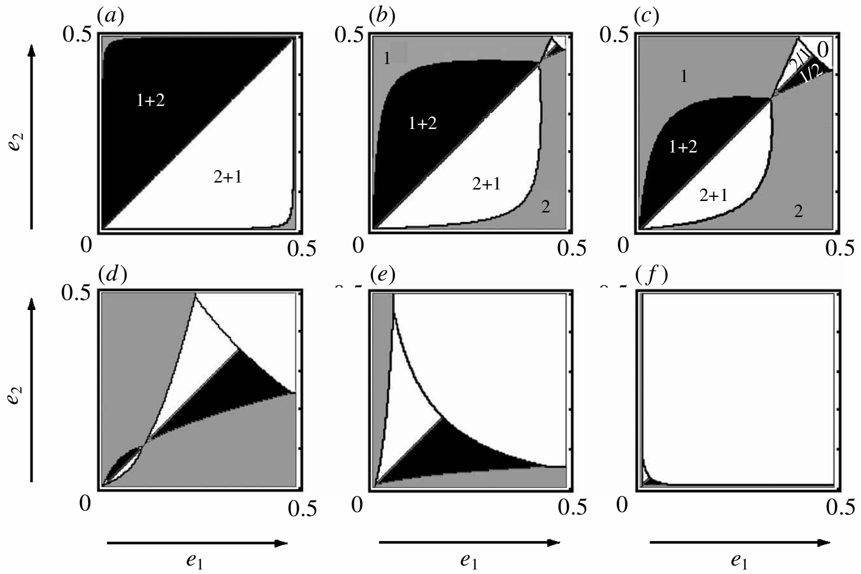

Figure 2. Optimal mate-assessment strategies for varying levels of the error in assessing cues, e_1 and e_2. The frequency of desirable males, f, is set at 0.2, and both assessment costs, a_1 and a_2, at 0.001. The six plots show the effect of increasing sampling cost c: (*a*) $c = 0$; (*b*) $c = 0.02$; (*c*) $c = 0.05$; (*d*) $c = 0.125$; (*e*) $c = 0.185$; and (*f*) $c = 0.1975$. Numbers on the plots indicate which cues are required by the strategy: 0, 'anyone'; 1/2, 'either-one'; 2/1, 'either-two'; 1, 'one'; 2, 'two'; 1+2, 'both-one'; 2+1, 'both-two'.

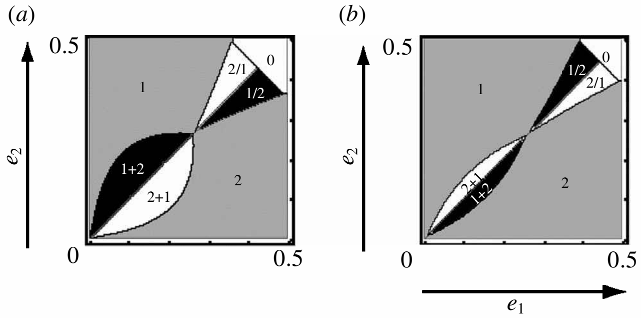

Figure 3. Optimal mate-assessment strategies for varying levels of the error in assessing cues, e_1 and e_2. The sampling cost, c, is set at 0.075 and both assessment costs, a_1 and a_2, at 0.001; (*a*) $f = 0.2$; and (*b*) $f = 0.8$. Numbers on the plots are as in figure 2.

accurate than the other. If both cues have low accuracy, it pays a female to accept the first male she meets ('anyone'). As the sampling cost increases further, this indiscriminate strategy is favoured even when one or both cues are highly accurate, until eventually it is the only optimal strategy however accurate the cues.

The 'both' and 'either' strategies are the ones that sometimes make use of multiple cues. As we have seen, these are favoured when sampling costs are relatively low and when the cues have reasonably similar accuracies. When it pays a female to use multiple cues, which cue should she prioritize in her assessment? This depends on whether the parameter values favour a choosy 'both' strategy or a less choosy 'either' strategy, and also on the frequency of desirable mates. Figure 3 shows the optimal strategies for an intermediate sampling cost, both when desirable mates are rare and when they are common. A highly choosy female requiring both cues ('both-one', 'both-two') should examine the more accurate cue first when desirable mates are rare, but the less accurate cue first when desirable mates are common. The reverse is true for less choosy females willing to accept a mate with either cue ('either-one', 'either-two'): when desirable mates are rare they look at the less accurate cue first, whereas when desirable mates are common they look at the more accurate cue first.

The order in which the cues are assessed has smaller consequences on fitness than a female's criteria for acceptance, unless the costs of assessment differ markedly. Figure 4 shows the effect of increasing the assessment cost for cue two while holding that for cue one constant. As a_2 rises, looking at cue one (the cheaper cue) first is favoured over more and more of the parameter space. If a_2 is sufficiently high relative to a_1, females considering multiple cues ('both' and 'either' strategies) should prioritize the cheaper cue regardless of the relative accuracy of the cues.

We can summarize these results mathematically by finding the conditions under which looking at cue one first is favoured over looking at cue two first. For the 'both' strategies, $W_{\text{both-one}} - W_{\text{both-two}} > 0$ holds for

$$\frac{a_1}{a_2} < \frac{(1-e_1)(1-f)+e_1 f}{(1-e_2)(1-f)+e_2 f}. \tag{3.1}$$

If the assessment costs are equal or sufficiently similar, the ratio a_1/a_2 will be close to unity. When $f < 0.5$, the right-hand side of inequality (3.1) will be greater than one when cue one is more accurate ($e_1 < e_2$) but less than one when cue two is more accurate ($e_1 > e_2$). A female accepting only males with both cues should therefore look at the more accurate cue first. When $f > 0.5$, however, the right-hand side will be less than one when cue one is more accurate but greater than one when cue two is more accurate, and therefore the female should look at the less accurate cue first.

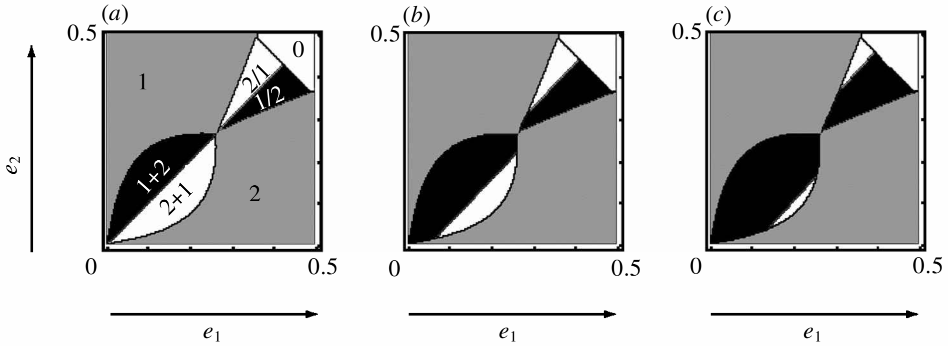

Figure 4. Effect of increasing one assessment cost, a_2, on the optimal mate-assessment strategies for varying levels of the error in assessing cues, e_1 and e_2. The frequency of desirable males, f, is set at 0.2, the sampling cost, c, at 0.075 and the cost of assessing cue one, a_1, at 0.001; (*a*) $a_2 = 0.001$; (*b*) $a_2 = 0.00104$; and (*c*) $a_2 = 0.001\,085$. Numbers on the plots are as in figure 2.

If one cue is much more costly to assess than the other, the ratio a_1/a_2 will be very different from unity and inequality (3.1) will hold only if cue one has the lower assessment cost. Under these circumstances, a female requiring both cues should examine the cheaper cue first, regardless of its accuracy.

When $f = 0.5$, the right-hand side of inequality (3.1) will be one regardless of the values of e_1 and e_2. In this case the female is always better off assessing the cheaper cue first.

Turning to the less choosy 'either' strategies, $W_{\text{either-one}} - W_{\text{either-two}} > 0$ holds for

$$\frac{a_1}{a_2} < \frac{f + e_1(1 - 2f)}{f + e_2(1 - 2f)}. \tag{3.2}$$

As before, if the assessment costs are equal or sufficiently similar, the ratio a_1/a_2 will be close to unity. When $f < 0.5$, the right-hand side will be less than one when cue one is more accurate but greater than one when cue two is more accurate; therefore a female accepting males with either cue should look at the less accurate cue first. When $f > 0.5$, the right-hand side will be greater than one when cue one is more accurate but less than one when cue two is more accurate, and therefore she should look at the more accurate cue first.

If the cues differ markedly in assessment cost, a female looking for a male with either cue is better off examining the cheaper cue first, regardless of its accuracy.

When $f = 0.5$, the right-hand side of inequality (3.2) will be one regardless of the values of e_1 and e_2. In this case the female is always better off assessing the cheaper cue first.

4. DISCUSSION

The model enables us to predict the optimal mate-choice behaviour of females when males possess multiple cues, and to investigate how this changes in relation to sampling costs, assessment costs, cue accuracies and the abundance of desirable mates.

As the sampling cost increases, females should become less choosy. This has been predicted by other theoretical treatments (e.g. Real 1990; Reynolds & Gross 1990; Getty 1996) and makes intuitive sense: if it is costly to locate each successive male, a female cannot afford to reject too many of them. There is evidence that this is the case in nature (e.g. Alatalo *et al.* 1988; Milinski & Bakker 1992; Hedrick & Dill 1993).

Provided that the cues have similar accuracies, females should be more choosy when desirable males are common. In such circumstances there is a high chance that a female will meet a desirable male after only a few encounters, so it pays her to be selective and to reject males lacking the cues she is looking for. Consistent with this prediction is the idea that females are more choosy after exposure to several high-quality males. Collins (1995), for example, found that female zebra finches (*Taeniopygia guttata*) showed a stronger preference for a male displaying at a high rate after exposure to other males with high display rates. An interesting extension of our model would be to investigate this kind of effect explicitly, allowing a female's decision rule to be modified by experience (e.g. Dombrovsky & Perrin 1994; Mazalov *et al.* 1996).

How many cues should a female use in mate assessment? If there is zero cost to assessing cues, a female should not restrict her assessment to a single cue but should make use of all the available information. When cues are costly to assess, however, it can sometimes pay her to use only one cue. As assessment costs rise, such a strategy is increasingly favoured over strategies that use multiple cues.

When it pays a female to use multiple cues, which cues should she prioritize? When desirable mates are rare, the choosy 'both' strategy looks at the most accurate cue first, whereas the less choosy 'either' strategy looks at the least accurate cue first. When desirable mates are common, the situation is reversed. The reason for this difference is that both types of female want to minimize the costs they incur before finding their desired mate, but they do so in different ways. First, consider females playing the strategy 'both'. Whether they accept or reject an encountered male does not depend on the order in which they assess his cues. If he lacks one or both cues, however, the costs they incur in rejecting him depend critically on the order of assessment. Clearly, to minimize the costs they pay, they should first examine the cue that is less likely to be present, as this avoids an unnecessary second assessment cost.

Now consider females that are happy to accept males with either cue ('either'). Again, the order in which they assess a male's cues has no effect on whether they will accept or reject him, but it does affect the costs they pay. In contrast to the 'both' strategy, however, 'either' females should simply go for the cue that is most likely to be there.

If the male has this cue they can terminate their search without considering a second cue.

Which cue is more common is determined by the frequency of desirable mates and the relative accuracy of the cues. When desirable mates are rarer than undesirable mates, the more accurate cue is less likely to be present. When desirable mates are more common, by contrast, the less accurate cue is less likely to be present.

Prioritization of cues also depends on assessment costs. If one cue is much cheaper to assess than the other, such that the ratio a_1/a_2 is markedly different from one, it will always pay females to look at this cue first even if it is much less accurate. Clearly there is a lot less for the female to lose by looking at this cue first.

Our model leads to a number of predictions. First, cue prioritization is altered by the sampling cost. Several experiments (e.g. Alatalo *et al.* 1988; Milinski & Bakker 1992) have successfully manipulated sampling cost, so it should be possible to test whether this changes the cues that are most important to females in mate choice.

Manipulation of assessment costs is likely to be somewhat more problematic. However, there is already evidence to suggest that, where the cues of a multicomponent display seem to have vastly different assessment costs, females begin by examining the cue that is cheaper to assess. Females of the fiddler crab *Uca annulipes*, for example, make an initial assessment of male quality based on size and then make a final mating decision using burrow characteristics (Backwell & Passmore 1996). Similarly, in the village weaverbird (*Ploceus cucullatus*), females initially accept a male on the basis of his nest-invitation display, but may reject him several days later if his nest is poorly constructed (Collias 1979). In both examples, the time cost associated with assessment of the first cue is markedly lower than that of the second cue. Courtship in humans may proceed along similar lines: initial quick judgements of a potential mate's suitability may be made largely on the basis of physical attractiveness, while assessment of personality takes place at a later stage (Miller & Todd 1998).

A final prediction concerns the prioritization of cues in relation to the frequency of desirable mates. This should be easy to test where two closely related species have overlapping geographical ranges, particularly if there is some risk of cross-species mating. As the relative abundance of conspecific (desirable) and heterospecific (undesirable) males changes across the zone of sympatry, the prioritization of mate-choice cues by females might change accordingly.

Previous models of mate sampling (e.g. Janetos 1980; Parker 1983; Real 1990) have improved our understanding of female choice, but have neglected the costs of cue assessment and the additional complications raised by multiple cues. Here, we have shown that female assessment of multiple cues may depend on the cost of locating males, the cost of assessing different cues, the accuracy of those cues and the frequency of desirable males, all of which may vary within and between species. Our model is applicable to many discrimination tasks in nature and provides a first step towards understanding how choosers make sense of the information contained in complex multicomponent stimuli.

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