

The empirical question of thresholds and mechanisms of mate choice

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Summary

Theoretical discussions concerning how animals might best sample and select mates have suggested that individuals could base decisions either on a sample of mates (sample-based decisions) or on a threshold of comparison (threshold-based decisions). Recent theoretical work demonstrates that threshold-based mating decisions generate higher expected fitness than sample-based mating decisions when search costs exist. Empirical results from most unmanipulated systems, however, either conclude that females make sample-based decisions or are inconclusive. A few experimental studies designed to detect mating thresholds purport to demonstrate threshold-based choice but an examination of these studies indicates such conclusions were premature. We believe that few examples of threshold-based choice exist because protocols designed to identify mating thresholds were often inconsistent with models of threshold choice. We suggest that future empirical work strive not to document mating thresholds *per se*. Rather, future work might best reveal decision rules by manipulating the distribution of quality among potential mates; such manipulations predict uniquely how females using sample-based and threshold-based decision rules should behave.

Keywords: decision rules; mate choice criteria; sample-based decisions; threshold-based decisions; sexual selection

Introduction

Decision-making is often a two-step process. First, information is used to discriminate differences of various alternatives. The second step of a decision employs a rule to evaluate and select the most profitable option.

Animals make many kinds of choices but here we focus on how individuals choose mates. Depending on the system, either sex may mate selectively, but for simplicity we focus on the mating decisions of females. Consider a female that encounters a single potential mate and must choose whether or not to mate with him. To decide, the female must first assess the male's quality. Let us assume she can do this by evaluating certain traits which we assume to be honest indicators of his fitness (e.g. Kodric-Brown and Brown, 1984; Arnold, 1985). Having estimated the male's quality, she then must decide whether his quality warrants mating. In the mate choice literature, a great deal of past work has focused on determining which particular male traits females use to estimate male quality (e.g. Lande, 1981; Hamilton and Zuk, 1982; Bateson, 1983; Boake, 1986; Bradbury and Andersson, 1987). Only recently has attention turned to female

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decision rules, i.e. the process by which females reject and accept mates (e.g. Janetos, 1980; Parker, 1983; Wittenberger, 1983; Real, 1990).

Four commonly described decision rules are (1) best of n – a female samples n males and selects the one of highest quality (Janetos, 1980), (2) sequential comparison – a female chooses the best male from only the two most recently sampled (Wittenberger, 1983), (3) fixed threshold – a female mates with the first male whose quality is above some minimum criterion (Janetos, 1980; Wittenberger, 1983) and (4) one-step (or sequential search) – a female mates with the first male whose quality is greater than the expected quality of future potential mates (Janetos, 1980; Real, 1990).

These four decision rules can be divided into two categories based on an assumption about the criterion that a female uses to make her decision. The first two decision rules assume that the female's decision is based on only a sample of males. The best of n rule assumes a sample of n males, while sequential comparison assumes a sample of just two males. The latter two decision rules, fixed threshold and one-step, assume that the female's decision is based on a threshold of acceptability. In the first case, the threshold is genetically fixed. In the second, a female must determine whether the expected fitness to be gained by accepting the current potential mate is greater than the expected fitness to be gained by continuing to search for a mate (Real, 1990). To make this decision, information about the whole population of potential mates is used to generate the acceptance threshold. Such population information might include the mean or variance in the quality of males in the population (Janetos, 1980; Real, 1990).

These decision rules have often been described using the terms relative and absolute choice. Most often, decisions based on a sample of males have been equated with the term 'relative' choice while decisions based on thresholds have been equated with the term 'absolute' choice (e.g. O'Donald, 1980; Zuk *et al.*, 1990). Alternatively, some authors have used the terminology 'comparison to an external standard' to refer to relative choice and 'comparison to an internal standard' to refer to absolute choice (Moore and Moore, 1988; Hoikkala and Aspi, 1993).

Unfortunately, the terms relative and absolute have led to much confusion in the literature (see Zuk *et al.*, 1990). For instance, Brown and Downhower (1983) described both absolute and relative mating decisions but used these terms in a different context. They described how a female might select the best male in either an absolute or relative sense. A female choosing the best male in an absolute sense uses a best of n decision rule where n is the entire population of males; a female choosing the best male in a relative sense also uses a best of n decision rule where n is just a subset of the population of males. Another example of confusion regarding these terms occurs in Lande (1981). Lande (1981) used the term 'relative preference' to describe female choice relative to the mean value of a male character in the population. This definition, however, is equivalent to an absolute decision rule where the threshold of acceptability is the mean value of a male character in a population (e.g. Janetos, 1980).

It is likely that confusion has arisen because in both relative and absolute choice, a decision is made relative to some standard, either other sampled males or a threshold. Therefore, instead of using the terms relative and absolute choice, we will emphasize the distinction between these alternatives by focusing on the difference in decision criteria: decisions based on a sample of mates will be called sample-based and decisions based on a threshold will be called threshold-based.

Additional confusion surrounds attempts to distinguish empirically sample-based from threshold-based mating decisions. Numerous attempts have been made, both in unmanipulated and experimental systems, to determine whether female mating decisions are based on a limited sample of males or a threshold (Brown, 1981; Brown and Downhower, 1983; Foote, 1988; Moore and Moore, 1988; Slagsvold *et al.*, 1988; Trail and Adams, 1989; von Scantz *et al.*, 1989; Dale

et al., 1990, 1992; Zuk *et al.*, 1990; Bakker and Milinski, 1991; Petrie *et al.*, 1991; Bensch and Hasselquist, 1992; Palokangas *et al.*, 1992; Choudhury and Black, 1993; Hoikkala and Aspi, 1993; Downhower and Lank, 1994; Fiske and Kalas, 1995).

Studies of unmanipulated systems often have examined female search patterns including the position of the chosen male in the sequence of males observed and whether or not males were revisited by females. Essentially all of these studies have concluded that females use a sample-based decision rule. In a recent examination of several field studies of mate choice, however, Wiegmann *et al.* (1996) noted that the data used to distinguish sample-based from threshold-based decisions were often ambiguous. In fact, Wiegmann *et al.* stated that the data used to demonstrate sample-based choice could often be interpreted as providing stronger support for a threshold-based decision. Wiegmann *et al.* concluded that experimental work should provide better discrimination for determining whether females make sample- or threshold-based mating decisions.

Unlike studies of unmanipulated systems that have consistently concluded that females make sample-based decisions, some experimental studies of mate choice have concluded that females make threshold-based decisions (e.g. Moore and Moore, 1988; Zuk *et al.*, 1990; Hoikkala and Aspi, 1993). Given the ambiguous nature of the conclusions drawn from studies of unmanipulated systems (Wiegmann *et al.*, 1996), we decided to examine three recent experimental studies that have concluded that females make threshold-based mating decisions. The goal of our examination is not to question earlier work, but to shed light on how future empirical work can best be directed. We begin our examination of mate choice decision rules with a brief review of the concept of a mating threshold.

What is a mating threshold?

The concept of a mating threshold or a threshold of acceptability is based on a female's response function that describes the relationship between female behaviour and the quality of potential mates. The response function can provide evidence of a threshold when it takes the form of a step function: below some critical (threshold) value of male quality, females do not mate, while above the critical value, females mate with a male (Real, 1990). All step functions 'exhibit points of discontinuity where the function suddenly jumps from one value to another without taking on any of the intermediate values' (Thomas, 1972, p. 25). Note that the key aspect of step functions is their discontinuity. The alternative to a step function is a continuous function. Among other criteria, a continuous function is one that does not exhibit jumps from one value to another (for a precise definition, see Thomas (1972, p. 97)).

Two kinds of data are typically recorded in empirical studies of mate choice. In some studies, females are allowed to mate with males and so such studies yield information about mated (i.e. accepted) and unmated (rejected) males. Occasionally such data are recorded as the proportion of mating success for various types of males (e.g. Hoikkala and Aspi, 1993). Other studies do not allow females to mate with males but instead record the strength of a female's preference for different males (e.g. Foote, 1988). Preference is usually determined by recording the amount of time a female spends in association with different males because time in association is assumed to correlate with actual mating preference (e.g. Kodric-Brown, 1989).

The kinds of data recorded in mate choice studies can have implications for observing mating thresholds. Discrete data, such as accepting or rejecting a mate, can clearly exhibit points of discontinuity, the distinguishing feature of threshold choice. Continuous data, such as time in association, however, may rarely exhibit discontinuities. Such data, therefore, can make the identification of mating thresholds more difficult (Fig. 1).

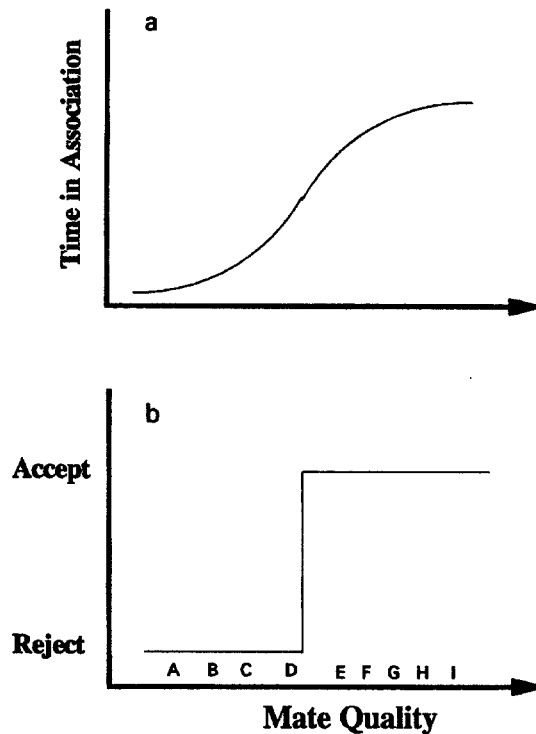


Figure 1. Schematic representation of two kinds of mate choice response functions. In each case the x -axis is the quality of potential mates. Letters refer to different males a female might observe. (a) The y -axis represents continuous behavioural data such as percent time in association and does not contain a discontinuity. (b) The y -axis represents discrete behavioural data such as accept or reject as a mate. The example here shows that a female rejected males A–D while mating with males E–I. The female response function contains a discontinuity.

Previous experimental attempts to document mating thresholds

Jungle fowl. One of the often cited examples of threshold choice is the work of Zuk *et al.* (1990). In their work, however, they described a threshold choice that differs substantially from that depicted in Fig. 1. Zuk *et al.* (1990, p. 478) stated that threshold choice occurs when a female has a threshold level of acceptability for a male trait below which 'she will not exert her preference'. Thus, Zuk *et al.* concluded that if a female observes two males that are below the female's threshold, 'she will not prefer either, i.e., she will mate randomly with respect to the trait in question' (*ibid.*). This description of a mating threshold differs from Fig. 1 in two respects. First, it implies that females simultaneously choose between two potential males. Second, it assumes that the female mates with one of them. Thus, Zuk *et al.* (1990) do not allow for the possibility that a female would simply reject all males who possess undesirable traits.

Zuk *et al.*'s (1990) experiments follow their description of a mating threshold. Female jungle fowl (*Gallus gallus*) were exposed to two males simultaneously and data were discarded from the analyses if a female failed to mate with either male (Zuk *et al.*, 1990). In their analysis of female behaviour, Zuk *et al.* (1990) divided females into two groups. Fast-mating females mated quickly while slow-mating females took much longer to mate with one of the males. Because females mated with one of the two males in each trial, Zuk *et al.* (1990) compared chosen (mated) and

unchosen (rejected) males for each group of females. The mean comb length of chosen and unchosen males did not differ significantly for the slow-mating females but the mean comb length of chosen males was significantly longer than unchosen males for the fast-mating females. From these data, Zuk *et al.* (1990) concluded that slow-mating females mated at random with respect to comb length whereas fast-mating females did not. Further, because the mean comb length of chosen males for fast-mating females was significantly longer than the comb length of chosen males for slow-mating females, Zuk *et al.* (1990) concluded that fast-mating females used a threshold decision rule to mate.

Given the differences between the description of a mating threshold provided by Zuk *et al.* (1990) and that of Fig. 1, the conclusion that fast-mating female jungle fowl make threshold-based mating decisions seems somewhat tenuous. First, it is unclear how a significant difference in the chosen male comb length of fast- and slow-mating females uniquely supports a threshold-based decision rule. Second, examination of data for fast-mating hens reveals that chosen males had significantly longer combs than unchosen males (Zuk *et al.*, 1990, table 1). Such data provide strong support for a best of 2, sample-based decision rule.

Zuk *et al.* (1990) did, however, present stronger evidence of threshold-based mate choice, but these data come from trials not included in the earlier analyses. In nine of the ten trials where females failed to mate, the female was confronted with a pair of males that had very short combs. This is precisely the behaviour predicted by the threshold-based choice model depicted in Fig. 1.

Cockroaches. Another protocol used to distinguish threshold- from sample-based mating decisions is to examine mating decisions of females presented with males one at a time. In these so-called 'no-choice' trials (Hoikkala and Aspi, 1993), it is assumed that if females reject the only male that they observe, they cannot be basing their decision on a sample of males but instead must be doing so based on an internal standard of comparison, i.e. a threshold (Moore and Moore, 1988; Hoikkala and Aspi, 1993).

Moore and Moore (1988) used such a protocol to examine mating decisions of a cockroach (*Nauphoeta cinerea*). Female cockroaches prefer to mate with dominant males. Moore and Moore (1988) observed that with only one (subordinate or dominant) male present, the female courtship behaviour was similar to courtship when two males (one subordinate and one dominant) were present; in each case, females responded significantly more slowly to subordinate males compared with dominant males.

Models of threshold-based choice assume that females encounter males one at a time (Real, 1990) and so no-choice trials should be a powerful protocol for detecting mating thresholds. Such models predict that if females encounter a male whose quality is below the mating threshold, he should not be accepted as a mate. The behaviour of female cockroaches, however, did not correspond to such a model. While Moore and Moore (1988) showed that females responded significantly more slowly to subordinate males than to dominant males even when presented alone, females did not reject such males as mates. They simply took longer to court them. Thus, while female behaviour prior to mating differed based on male status, it seems premature to conclude females were using a threshold-based decision rule to make mating decisions.

Fruit flies. Hoikkala and Aspi (1993) conducted both no-choice and simultaneous choice trials with three species of fruit flies. They recorded the mating behaviour of females in the presence of one or two males who had been experimentally altered. To determine whether females made threshold-based mating decisions, Hoikkala and Aspi (1993) compared the mating success of males in no-choice experiments to similar data from simultaneous choice trials.

Hoikkala and Aspi's (1993) work clearly demonstrates a mating threshold for *Drosophila montana*: when the wings of males were completely removed, females always rejected them as mates (their Fig. 3). Males with intact or partially removed wings were accepted as mates in more than 80% of the experimental trials. Hoikkala and Aspi (1993) also concluded that female *Drosophila ezoana* exhibited a mating threshold. In this species, however, wingless males were not always rejected as mates: approximately 30% of wingless males obtained matings. In both cases, however, it is possible that females rejected wingless males not because they perceived them as poor mates, but rather because they could not recognize them as possible mates; the ability of wingless males to produce courtship sounds was severely hampered (Hoikkala and Aspi, 1993).

Guidelines for future empirical work

Theoretical comparisons have shown that search costs critically influence whether sample-based or threshold-based decisions generate a higher expected fitness. If search costs are zero, a sample-based (best of n) decision rule yields a higher expected fitness than a threshold-based (sequential search) decision rule (Janetos, 1980; Real, 1990). Real (1990), however, demonstrated that for all non-zero search costs, the sequential search model yielded a higher expected fitness than a best of n rule and that the difference in expected fitness between these rules was largest at intermediate search costs.

Given that threshold-based mating decisions yield a higher fitness than sample-based mating decisions when there are search costs, why have so few empirical studies demonstrated threshold-based mating decisions? Our examination of recent experimental empirical work provides possible answers to this question: different workers have applied different assumptions, protocols and techniques in attempting to document threshold-based choice.

To distinguish sample- from threshold-based mating decisions requires that females be exposed to males one at a time. Recall that theoretical models of threshold-based decisions assume that females can benefit by rejecting the currently encountered potential mate because if they continue searching they will likely encounter one that is of higher quality (e.g. Real, 1990). While this sequential process is assumed in models of threshold-based choice (e.g. Real, 1990), it is not always employed in empirical tests (but see Moore and Moore, 1988; Hoikkala and Aspi, 1993; Downhower and Lank, 1994) where, quite often, females are allowed to view mates simultaneously (e.g. Wilkinson, 1987; Foote, 1988; Zuk *et al.*, 1990).

The problem with simultaneous choice is that it reduces the costs of searching for mates essentially to nil. Threshold-based decision rules generate a higher expected fitness than sample-based decision rules only when search costs exist (Real, 1990; Wiegmann *et al.*, 1996). Thus, when mate-searching costs are minimal, as in simultaneous choice protocols, females might be expected to use a sample-based decision rule (Real, 1990). Simultaneous choice protocols, therefore, may severely bias results in favour of finding a sample-based mate choice. Perhaps this explains why sample-based mate choice has been observed frequently (e.g. Brown and Downhower, 1983; Wilkinson, 1987; Bakker and Milinski, 1991), while threshold-based choice has not (but see Hoikkala and Aspi, 1993).

Granted, it can be difficult to devise a protocol ensuring that females 'know' they will encounter additional potential mates after rejecting the current male. Simultaneous male presentations may circumvent this problem, but, as noted above, can introduce an important bias. If simultaneous presentation protocols are used, care must be taken to allow females the opportunity to reject all mates in a given experimental trial because trials where females reject all males are as important as trials in which one of the males is accepted. Trials in which females

reject all males can be strong evidence for a mating threshold when the rejected males are of low quality.

The alternative to simultaneous male presentation protocols are no-choice trials in which females observe males one at a time. Again, in this protocol it is crucial that females are allowed to benefit by rejecting the current male (i.e. females must 'know' that they will have the opportunity to search for better mates). Otherwise, threshold-based decision rules will be difficult to identify. Constraining females to mate with presented males is at odds with a fundamental assumption of threshold-based models of mate choice; females must be allowed to reject current males to search for one that is more preferred (Real, 1990).

Given the difficulties in devising protocols that allow females both to reject currently encountered male(s) and to know that future potential mates will be encountered, it seems likely that future work explicitly searching for mating thresholds will progress slowly. Are there alternative procedures for assessing whether females make sample- or threshold-based mating decisions?

Wiegmann *et al.* (1996) have recently outlined how mating decisions can be examined more directly. They demonstrate how changes in parameters pertaining to the population of males should influence the mating decisions of females that use different decision rules. For instance, changes in the mean or variance of the distribution of male qualities should result in predictable changes in the threshold criterion of acceptance (see also Real, 1990). Such manipulations of the distribution of quality of potential mates generate unique predictions for the behaviour of females using sample-based and threshold-based mating decisions. Manipulations of population parameters will not be easy. One possible method is to raise females in view of populations of males that differ in the mean or variance of some trait used by females to discriminate between males. One can then determine if females raised under these different conditions make different mating decisions (Real, 1990; see also Nordell, 1995).

Implications

Several authors have discussed how the mechanism of female choice (i.e. use of sample- or threshold-based decision rules) can have a profound influence on the evolution of secondary sexual traits (O'Donald, 1980; Lande, 1981; Seger, 1985; Zuk *et al.*, 1990). In particular, sample-based decision rules may impede the genetic correlation between the female preference for a male trait and the trait itself (Zuk *et al.*, 1990) as required in runaway sexual selection models (Fisher, 1930) and can lead to unstable lines of equilibria between these factors in simple genetic models (Seger, 1985). This can occur because females using sample-based decision rules may mate with males of rather low quality more often than females using threshold-based decision rules (Zuk *et al.*, 1990).

Given the theoretical demonstration that threshold-based decisions generate a higher expected fitness than sample-based decisions when search costs are present (Real, 1990) and the potential implications for the evolution of sexually selected traits, it is of interest that threshold-based mating decisions have been so rarely identified compared with sample-based decisions. Our examination of recent experimental empirical work suggests that even those few studies cited as documenting threshold-based choice may have been premature in their conclusions. Clearly, additional empirical work is required to understand more fully the prevalence of threshold- and sample-based mating decisions to gain further insight into the evolution of secondary sexual traits.

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