



Mate choice rules in animals

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We identify several fundamental properties of how females choose mates and propose statistical methods to test hypotheses about them. Virtually, all studies of mate choice have implicitly assumed that choice involves what we call strict preference. By that we mean that all the properties of a stimulus can be reduced to a single preference value that is independent of other stimuli, and that the stronger a female's preference for a male, the more likely she is to choose him. An important consequence of strict preference is that it guarantees that females cannot show intransitive choice (where male X_1 is preferred over male X_2 , and X_2 over X_3 , but X_3 is preferred over X_1). We find general conditions for the strict preference paradigm to apply in the simple situation where females choose between two potential mates. We illustrate how these conditions can be tested statistically using data on mate choice in túngara frogs, *Physalaemus pustulosus*. The results were not consistent with any of the standard models for strict preference. On the other hand, we also failed to find statistical support for intransitive choice. We suggest that understanding mate choice will require deeper analysis of the most basic properties of the choice rules.

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Many behaviours of animals emerge from choices: wake or sleep, eat or fast, reproduce or reabsorb, pair bond or cuckold. Although behavioural biologists know little of the neural algorithms underlying choice, we act as if we do. For example, preference functions are used to describe how females respond to variation in mating signals. These preference functions are then used to construct models for the evolution of the signal and preference, to intuit selection gradients and landscapes, and to design experiments for measuring female preferences.

But all of these research activities are founded on the implicit and untested idea that choice can be described by a preference function that ranks all males on a one-dimensional scale (Heisler et al. 1987; Jennions & Petrie 1997). The validity of this assumption is by no means guaranteed. It is possible, for example, that a female's response to a male is context dependent in a manner that cannot be captured by a single preference score. It is fair to say we know little about the validity of the assumptions underlying the paradigms used to study mate choice, or the theoretical consequences of violating those assumptions.

There is a well-developed literature on human decision making. Initially, workers assumed that decisions are based on a 'utility' score assigned to every object independent of all other objects (von Neumann & Morgenstern 1947; Luce 1959). This is equivalent to the preference function paradigm that is universal in studies of sexual selection. Later studies showed that humans can behave in ways inconsistent with that paradigm. In some settings, for example, subjects consistently show intransitive choice: object X_1 is chosen over X_2 , and X_2 over X_3 , but X_3 is chosen over X_1 . This discovery has had major impacts in economics and psychology (Tversky 1969; Navarick & Fantino 1972; Ng 1977; Tversky & Simonson 1993).

In contrast, the existence, causes and consequences of complex choice behaviours have not been well explored in the field of mate choice. At a mechanistic level, it is plausible that intransitive outputs would emerge from complex systems such as neural networks. Intransitive choice behaviours have been found in contexts other than mating, starting with work by Navarick & Fantino (1972) on pigeons. Intransitive biological interactions are also known in settings outside of choice behaviours, for example, in spatial competition among marine invertebrates (Buss 1980), territorial competition in lizards (Sinervo & Lively 1996), sperm competition in flies (Clark et al. 2000) and ecological competition in bacteria (Kerr et al. 2002). In summary, there is evidence from a variety of

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biological systems for intransitivities. This seems reason enough to consider the possibility that complex rules might be used by females during mate choice.

The discovery of intransitive mate choice could have major implications for sexual selection. It would suggest new hypotheses for the maintenance of mating strategy polymorphisms, for example, and for the divergence of sexual displays between populations. We return to these possibilities in the [Discussion](#).

The main goals of this study were to identify basic properties of choice rules that determine whether outcomes like intransitivity are possible and to introduce statistical methods to test for strict preference and for intransitive choice. We found the necessary conditions for mate choice to obey 'strict preference', which, if satisfied, guarantees that intransitive choice cannot occur. To illustrate these methods, we analysed a large data set on mate choice in túngara frogs, *Physalaemus pustulosus*. We found that all of the choice functions assumed in earlier models of mate choice could be rejected. These results do not support strict preference, but they also do not show evidence of intransitive choice. This leaves us without a clear picture of how mate choice works in these frogs, but we conclude that it does not operate by any of the standard choice rules. More generally, the methods developed here may be useful for further studies in a variety of systems.

This paper focuses throughout on binary choices. This is an appropriate context to begin discussing preference rules because it is the simplest. Binary choice experiments best test the hypothesis that there are 'just meaningful differences' between stimuli, the behavioural analogue of 'just noticeable differences' in psychophysics (Nelson & Marler 1990), and the results of binary choice tests can predict results in single choice tests (Phelps et al. 2006). Because one goal of mate choice studies is to determine the degree to which variation in male traits influences female choice, the binary choice test is a widely used experimental paradigm. Animals often choose between more than two potential mates, however. Many of the ideas and methods discussed here extend in a natural way to situations involving choice between three or more alternatives. In any event, we expect that the universe of possible outcomes in those situations is even more complex than what occurs with simple binary choice. We will return to this question in the [Discussion](#).

THEORETICAL BACKGROUND

This section introduces the four key concepts: a choice function, a preference function, strict preference and intransitive choice. The terms 'choice' and 'preference' are typically used in animal behaviour in a very general sense. Here, however, we will restrict these words to much more narrow definitions. We discuss stimuli that vary quantitatively, but many of the conclusions also apply to categorical (discrete) variation. By 'stimulus' we mean any combination of sensory inputs that a female receives, for example, from a potential mate or from speakers in an experimental arena. Stimuli may vary in more than one

parameter, for example, frequency and amplitude. For simplicity, we assume that the outcome of each trial is independent of previous experience. Mate choice in many animals is influenced by experience, of course, and we expect that the range of possible outcomes will be only more complex when that occurs.

Choice Functions

We will use the term 'choice' to refer to any outcome from a binary trial in which the animal shows taxis towards, affiliation with, or heightened response to one stimulus rather than another. We reserve the term 'preference' for certain kinds of choice rules that we will introduce shortly. Binary choice can always be quantified by the 'choice function' $C(X_1, X_2)$, defined as the probability that stimulus X_1 is chosen when competing against stimulus X_2 .

An example of a simple choice function based on a single parameter is shown in [Fig. 1](#). The X axis and Y axis give the values of the focal and competing stimuli, s_1 and s_2 , while the Z axis gives the probability C that the focal stimulus is chosen. We have oriented the plot such that values for the competing stimulus on the Y axis become larger as the axis extends from the page (towards the viewer). If stimuli differ in more than one parameter, then a plot of the choice function would conceptually require one axis for each parameter in the focal stimulus, one for each in the competitor, and a final axis for the probability that the focal stimulus is chosen.

Preference Functions

It is commonly assumed that mate choice is based on a 'preference function', which we denote $p()$. The idea here is that the effects on a female's choice of all the different aspects of a stimulus X can be reduced to a single

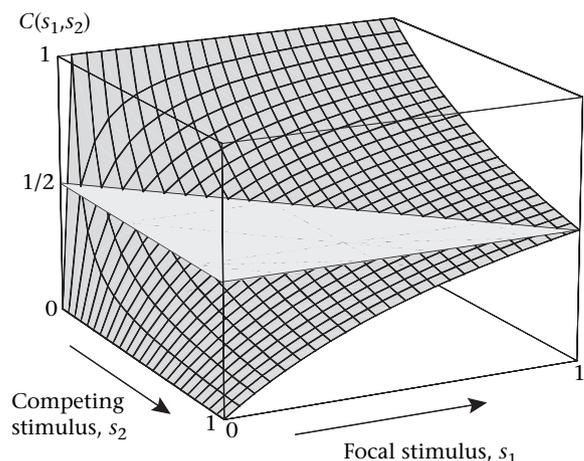


Figure 1. An example of a simple choice function: the relative choice function, $C(s_1, s_2) = s_1 / (s_1 + s_2)$. The horizontal surface shows the plane at which the two choices are equally likely. The focal stimulus with value s_1 is more likely to be chosen than the competing stimulus with value s_2 when the gridded surface lies above this plane.

preference value, $p(X)$, that is independent of the stimulus it is compared against.

Two examples of preference functions that depend on a single stimulus parameter s are shown in the two panels in the top row of Fig. 2. The simplest preference function, shown at the left, is linear. Response to signal amplitude over a small range of intensities typically takes this form. Another form of preference function follows a Gaussian function, shown on the right. Responses to variation in the frequency of visual and acoustic signals often approximate this form. (The 'tuning curves' often studied in sensory physiology are simply inverted versions of this type of preference function.) This example makes the point that preference functions can be nonmonotonic, showing a maximum (or minimum) for some intermediate value of the stimulus.

Knowing a female's preference for two stimuli is not sufficient to determine how she will choose between them. For that, we also need to know the choice function. In the left column of Fig. 2 are two choice functions. Here the functions are represented in terms of how choice depends

on the two preferences, $p(s_1)$ and $p(s_2)$, for the two stimuli values s_1 and s_2 that are being compared. With the 'absolute choice function', the most preferred stimulus is chosen without error. This decision rule has appeared in models of optimal foraging (Charnov 1976) and mate choice (O'Donald 1979). It is equivalent to the 'best-of- n ' choice rule (Seeger 1985) when only two stimuli are being compared.

With the 'relative choice function', the probability that stimulus X_1 is chosen over another stimulus X_2 is proportional to the relative strengths of the preferences that those stimuli evoke: $C(X_1, X_2) = p(X_1)/(p(X_1) + p(X_2))$. This function is shown in Fig. 1 and at the top right of Fig. 2. The relative choice function is by far the choice function that is most frequently assumed. It has been used in several fields, including psychology (Bradley & Terry 1952) and economics (Luce 1959), and has appeared in many models of sexual selection (e.g. Lande 1981; Kirkpatrick 1982). Other plausible choice functions can be proposed. We discuss one of them, based on the notion of perceptual error, below in our analysis of mate choice in frogs.

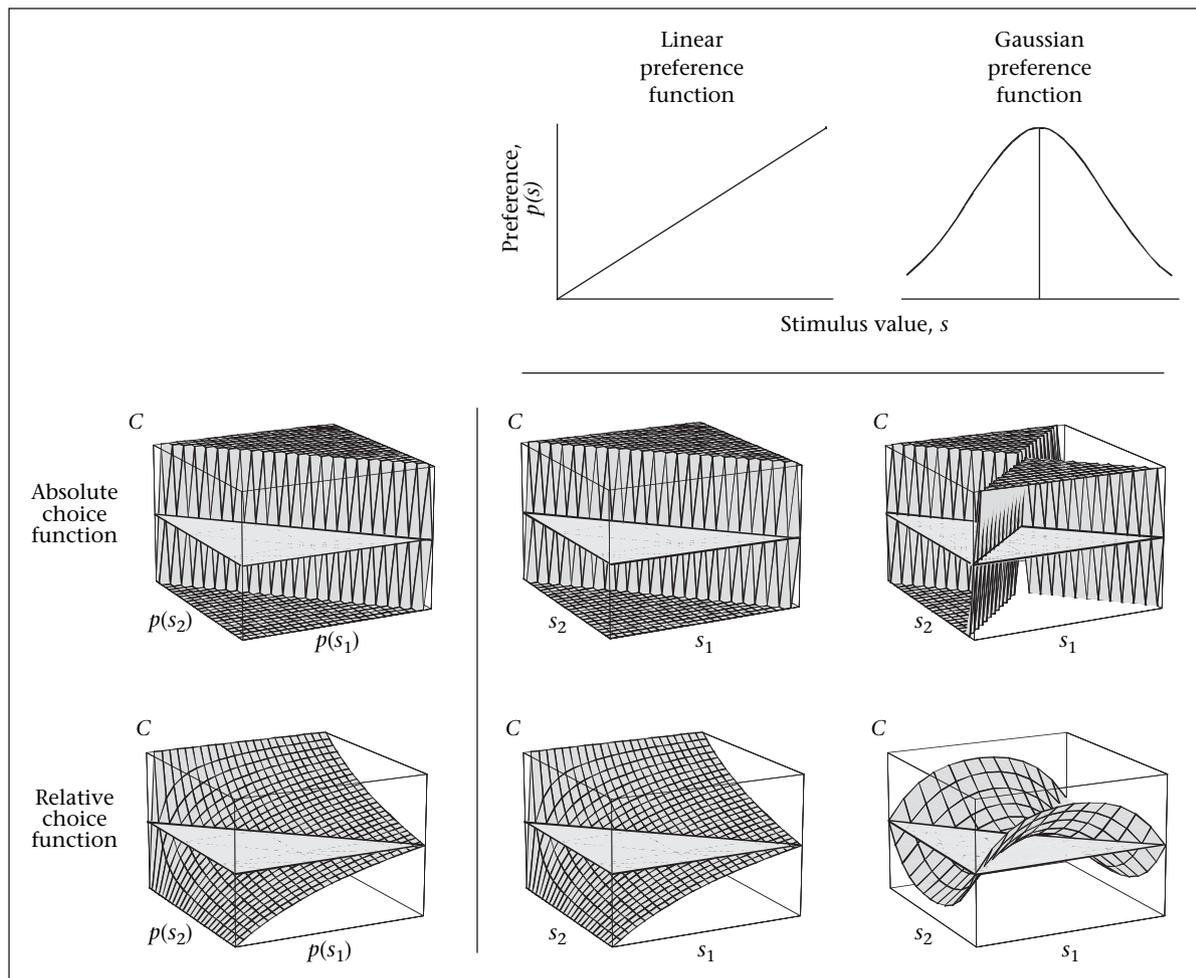


Figure 2. Examples of strict preferences that result from combinations of two preference functions and two choice functions. In the top row, the linear and Gaussian preference functions show how the preference p depends on the stimulus value s . In the left column, the absolute and relative choice functions show how C (the probability of choosing the focal stimulus) depends on the preference values $p(s_1)$ and $p(s_2)$ for stimuli s_1 and s_2 . The interior panels show how C depends on the two competing stimulus values s_1 and s_2 under the four combinations of preference function and choice function. See text for details.

While the left column of Fig. 2 shows the choice functions plotted in terms of the preferences for the competing stimuli, they can also be represented in terms of the values s_1 and s_2 of the competing stimuli (e.g. call frequency). Examples are shown in the four interior panels of Fig. 2. These show the outcomes that result from combinations of the choice functions in the left column and the preference functions on the top row.

Two conclusions can be drawn from Fig. 2. First, there is not necessarily a simple relation between the underlying preference and choice functions, on the one hand, and the observable outcome (that is, how choice varies with the values of the stimuli). Second, there are limited inferences we can make about choice rules from data on binary trials. With the absolute choice rule, for example, knowing that stimulus X_1 is chosen over X_2 and also over X_3 does not tell us what the outcome will be in a choice between X_2 and X_3 .

Strict Preference

Some kinds of choice obey what we call 'strict preference'. A key consequence of strict preference is that intransitive choice is not possible. In this section we define two conditions that result in strict preference. These conditions are equivalent to what is referred to in decision theory as a model with 'constant utility' and 'simple scalability' (Luce & Suppes 1965).

With strict preference, mate choice involves two steps. First, a female uses a preference function: the effects of all aspects of a stimulus are reduced to a single preference value that is independent of other stimuli (Criterion 1). Second, the female chooses a mate based on these preferences using a choice function that guarantees that a stimulus that is more preferred will be chosen more often than one that is less preferred (Criterion 2). Although this is a plausible scenario, we will see that it is not the only way that females might choose mates.

The first criterion for strict preference is that choice be based on a single score that is assigned to each stimulus. That is, that the effects on a female's choice of all the different aspects of a stimulus X can be reduced to a univariate preference value, $p(X)$. Thus, the choice function can be written in the following form.

Criterion 1 for strict preference (univariate preferences):

$$C(X_1, X_2) = f(p(X_1), p(X_2))$$

Here, $f()$ is simply the function that relates the preference scores $p(X_1)$ and $p(X_2)$ for the two stimuli X_1 and X_2 to the probability that X_1 is chosen. The point of the definition above is that this function depends only on two numbers, which are the preferences for the two stimuli. Criterion 1 is automatically met when the competing stimuli differ in only a single parameter, but does not necessarily follow otherwise.

The second criterion for strict preference is that as the preference for a stimulus increases, the probability that it is chosen must never decrease, regardless of what other

stimulus it is compared against. Formally, this means that the choice function must be monotonic in terms of the preference, as defined below.

Criterion 2 for strict preference (monotonic choice function):

$$\text{If } p(X_1) > p(X_2), \text{ then } C(X_1, X_3) \geq C(X_2, X_3) \text{ for all } X_3$$

Note that preference can be a nonmonotonic function of the stimulus' value (for example, call frequency) as long as this preference affects the outcome of choice in a monotonic way.

When choice is based on strict preferences, the choice function can always be visualized in three dimensions (two for the preferences of the competing stimuli, one for the probability of choice), even if the stimuli being compared vary in several parameters. (This is simply a reinstatement of Criterion 1 for preferences, which says that all stimuli can be assigned a single preference value.) This fact is useful in the analysis of mate choice trials, as we will see below.

What kinds of mate choice rules result in strict preference? All of the preference and choice functions shown in Fig. 2 satisfy the requirements for strict preference. This makes clear that a wide range of rules is possible, even though the criteria for strict preference place strong constraints on how choices are made. An intuition for Criterion 2 (a monotonic choice function) comes from looking at the choice functions in Fig. 1 and in the far left column of Fig. 2. Fix the competing stimulus for any particular value s_2 , and allow the value of the focal stimulus s_1 to increase. The probability C that the focal stimulus is chosen never decreases.

Transitive and Intransitive Choice

We expect that the outcome of binary choices between sets of stimuli will often be transitive. But intransitive choice has in fact been documented, as noted in the Introduction. Formal definitions of intransitivity have been developed in psychology and decision theory. We define 'strong stochastic intransitivity' as when stimulus X_1 is on average chosen over X_2 , X_2 over X_3 , and X_3 over X_1 (Tversky 1969). In terms of the choice function, this means that there must be at least one set of three stimuli such that the following condition is met.

Condition 1 for strong stochastic intransitivity:

$$C(X_1, X_2), C(X_2, X_3), C(X_3, X_1) > \frac{1}{2}$$

The term 'stochastic' means that the intransitivity is probabilistic: in any particular trial, intransitivity might not be observed, but it does occur on average. (Psychologists also talk of 'weak' stochastic intransitivity, but in the interests of simplicity we will not explore that idea here.)

What can be said about a choice function that causes intransitivity? First, intransitivity involving four or more stimuli implies that there must be an intransitivity within a subset of three of them (see Appendix). Thus, we can

understand what intransitivity implies about choice by considering only three stimuli.

Second, intransitivity has implications for the geometry of the choice function. When choice depends on only a single parameter of the stimuli, or if Condition 1 above is met, an intransitive choice function shows the geometry illustrated in Fig. 3. If the choice function is continuous and smooth, we can state the conditions for intransitivity based on the properties of the choice function at a single point. Intransitivity requires that there be at least one pair of stimulus values s_1 and s_2 that satisfy the following condition.

Condition 2 for strong stochastic intransitivity:

$$C(s_1, s_2) = \frac{1}{2} \text{ and } \left(\frac{\partial C(s_1, s_2)}{\partial s_1} \right), \left(\frac{\partial C(s_1, s_2)}{\partial s_2} \right) < 0$$

Two examples of such a point are indicated by the open circles in Fig. 3. This condition can be proven by a simple continuity argument discussed in the Appendix.

It may be easier to visualize the cause of intransitivity with the alternative perspective on the same situation shown in Fig. 4. Here we see that the effect of increasing the value of the focal stimulus depends qualitatively on the competing stimulus. Increasing the value of the focal stimulus makes it more likely that it will be chosen when faced with one type of competing stimulus. But increasing the focal stimulus has the opposite effect against another type of competing stimulus. This contrast is the source of the intransitive outcomes.

A key consequence of the two conditions for strict preference defined in the last section is that they provide sufficient conditions for transitive choice. The proof is equivalent to that for 'rational' choice behaviour (Luce & Suppes 1965). We have already seen from the example shown in Figs 3 and 4 that intransitivity can occur when Criterion 2 (monotonic choice function) is violated. To see that Criterion 1 (univariate preferences) can also

cause intransitivity, consider the following simple example (Tversky 1969). Say that choice is hierarchical and based on two components of the stimuli. The rule is to choose the stimulus with the larger value for the first component if the difference is greater than three, and if it is not then choose the stimulus with the larger value of the second component. Consider three stimuli for which stimulus X_1 has value (4, 0), stimulus X_2 has value (0, 2), and X_3 has value (2, 1). Stimulus X_1 is chosen over stimulus X_2 because of the difference in their first components. Stimulus X_2 is chosen over stimulus X_3 based on the second component. Last, X_3 is chosen over X_1 , again because of the second component.

Having outlined some of the basic features of binary choice, we now apply some of the concepts to analyse mate choice using data from túngara frogs.

MATE CHOICE IN TÚNGARA FROGS

We analysed the outcome of binary mate choice trials in the túngara frog to determine whether mate choice shows strict preference. If not, we wanted to determine whether choice is intransitive. In addition to establishing some facts about these frogs, we developed statistical methods that may be useful for analysing mate choice in other species.

We used female phonotaxis to mating calls as the bioassay to estimate a female's mate choice. This is an especially powerful bioassay since most female frogs only approach mating calls to select a mate. The data set, which consisted of multiple responses to all paired comparisons of nine stimuli, is large for animal mating preference studies and thus provides an unusually good opportunity to probe for interesting outcomes.

The Data

Full details of the experiments are reported in Ryan & Rand (2003), so we only summarize the main features

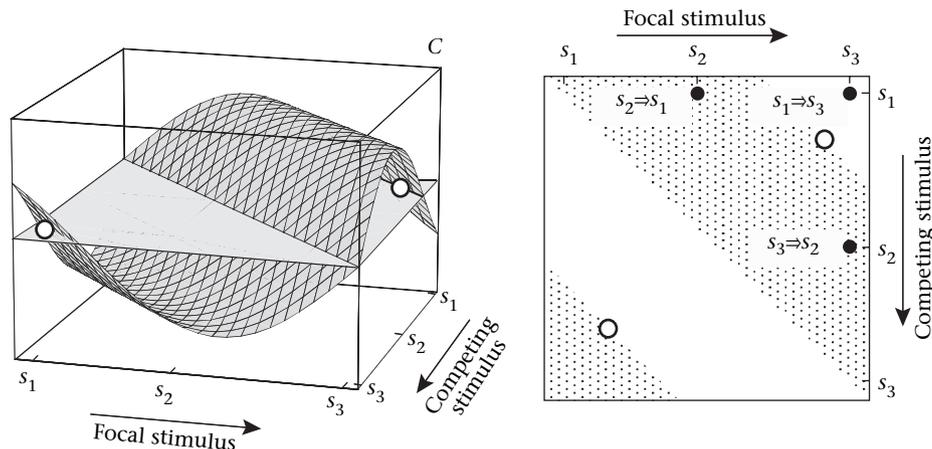


Figure 3. Example of a choice function that results in intransitive choice. On the left, the function is shown in three dimensions. On the right, the shaded regions are combinations of stimuli in which the focal stimulus is chosen more often than the competing stimulus. The solid points show an example of three stimuli that show strong stochastic intransitivity, with s_3 chosen over s_2 , s_2 over s_1 , and s_1 over s_3 . The open circles show points that satisfy Condition (2) for intransitive choice functions. For ease of visualizing the surface, the perspective for the left panel has been rotated from that of Figs 1 and 2.

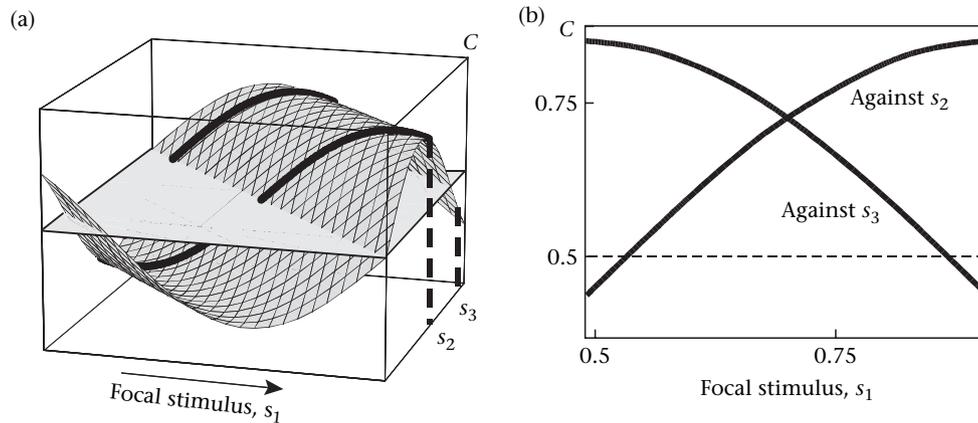


Figure 4. A different perspective on the choice function in Fig. 3 that produces intransitive choice. When competing against a stimulus with value s_2 , increasing values of the focal stimulus s_1 between 0.5 and 0.9 make it more likely that the focal stimulus is chosen. But when competing against a stimulus with value s_3 , increasing values of s_1 make it less likely that the focal stimulus is chosen. (a) Slices through the preference function corresponding to competing stimulus values s_2 and s_3 . (b) Two-dimensional graphs of those two slices over the focal stimulus range $0.5 < s_1 < 0.9$. In both panels, the vertical axis is the probability that the focal stimulus is chosen.

here. We recorded 300 calls from 50 males from a population of túngara frogs in Gamboa, Panama. We measured 15 variables of each call and used multidimensional scaling to identify patterns of variation. This analysis was used to choose a set of nine calls that represent the main axes of call variation in this population. These calls differ in many parameters.

Females' responses to these nine calls were tested in the laboratory. Calls were broadcast antiphonally from speakers in a sound-attenuation chamber that measured 1.8×2.7 m. Females were placed equidistant from the speakers. A positive phonotactic response was recorded if a female approached within 10 cm of one of the speakers.

We tested most females with several pairs of stimuli, but we were not able to test all females against all pairs of calls because females are receptive only for a relatively short period. Thus, the trials were not statistically independent of one another, nor did they represent repeated measures for individual females. However, there do not appear to be consistent differences between females in their response characteristics (Kime et al. 1998).

We analysed 20 responses to each pair of the nine stimuli, for a total of 720 choices. The results are shown in Table 1.

Do Túngara Frogs Show Strict Preference?

Our first question was whether the data were consistent with strict preference. Recall that we use the term strict preference to refer to choice that meets two criteria: females assign a univariate preference value to each stimulus regardless of the competing stimulus, and the probability that a female chooses a stimulus is an increasing function of that value.

We can test the hypothesis of strict preference statistically without knowing the rules that females use to calculate preference values, or even the properties of the stimuli, if we are willing to assume a specific choice function. We analysed the data under three choice functions consistent with strict preference. The first two were the absolute and

relative choice functions (Fig. 2) introduced in the last section. We will see that those hypotheses can be rejected. We therefore go on to consider a third choice function that includes an error component (either perceptual or experimental). This hypothesis will also be rejected.

We begin with the absolute choice function. Here, females choose the most preferred stimulus of a pair without error. Thus, for every pair of stimuli X_1 and X_2 , either $C(X_1, X_2) = 0$ or $C(X_1, X_2) = 1$. This model was rejected immediately, because there was not even a single pair of stimuli in Table 1 that showed this relationship.

Now consider the relative choice function. Under this hypothesis, if females have preferences p_1 and p_2 for two stimuli, the probability that they choose the first over the second is $p_1/(p_1 + p_2)$. Our approach to testing this hypothesis had two steps. We first used maximum likelihood to estimate the strength of preferences for each stimulus assuming that females use relative choice. We then tested the goodness of fit of the data to that model. The likelihood of the data, given the preferences for all the stimuli, was

$$L = \prod_i \prod_{j < i} B\left(n_{ij}; n_{ij} + n_{ji}, \frac{p_i}{p_i + p_j}\right) \quad (1)$$

where $B(n; N, P)$ is the binomial probability of n successes in N trials with probability P , and n_{ij} is the number of trials in which females chose stimulus X_i over stimulus X_j . We searched numerically for the values of p_i that maximized L using Mathematica v. 5.0 (Wolfram 2003).

The maximum likelihood estimates of the preferences for the stimuli in Table 1 are shown in Table 2. Under the relative choice rule, preferences can be scaled multiplicatively relative to any standard. Here we chose the least-preferred stimulus, S_c , as the reference and assigned it a value of 1.

If females use the relative choice rule, then their preference scores will predict the proportion of times that they will choose one stimulus over another in binary trials. The deviations from those predictions caused by sampling error

Table 1. Responses of female túngara frogs*

Focal stimulus	Competing stimulus								
	Sc	Sb	Ob	Oa	Oc	Sa	Sd	Od	M
Sc	—	0.5	0.4	0.35	0.3	0.35	0.2	0.25	0.15
Sb	0.5	—	0.35	0.6	0.4	0.2	0.05	0.25	0.2
Ob	0.6	0.65	—	0.4	0.5	0.3	0.4	0.4	0.1
Oa	0.65	0.4	0.6	—	0.5	0.5	0.2	0.2	0.45
Oc	0.7	0.6	0.5	0.5	—	0.75	0.5	0.4	0.1
Sa	0.65	0.8	0.7	0.5	0.25	—	0.3	0.55	0.45
Sd	0.8	0.95	0.6	0.8	0.5	0.7	—	0.25	0.4
Od	0.75	0.75	0.6	0.8	0.6	0.45	0.75	—	0.65
M	0.85	0.8	0.9	0.55	0.9	0.55	0.6	0.35	—

*Female responses in 20 paired choice trials to each pair of nine stimuli. Entry ij shows the fraction of times that females chose stimulus i over j in 20 trials (that is, the fraction of wins going to the stimulus listed at the left of that row). Bold values indicate pairs of stimuli where the responses were not in the expected direction. The stimuli are ordered from least preferred (Sc) to most preferred (M). The two-letter codes correspond to the stimuli described by Ryan & Rand (2003).

are determined by the binomial distribution, allowing us to test whether the data are consistent with the model. The rows and columns of Table 1 are arranged from the least to the most preferred stimulus. In the absence of sampling error, all entries above the diagonal will be less than $\frac{1}{2}$ and all those below will be greater than $\frac{1}{2}$. There were four pairs of stimuli that did not conform, but some exceptions are expected to result from sampling error. We then compared the observed choice frequencies with those expected from the relative choice model (Fig. 5).

We tested the relative choice model for goodness of fit to the data by comparing it against an alternative that we call the ‘unconstrained model’. Here, every pair of stimuli is assigned a choice probability independent of all other pairs. This is the most flexible possible statistical description of choice and it makes no assumptions (for example, that there are strict preferences).

With the unconstrained model, the maximum likelihood estimate for $C(X_1, X_2)$ is simply the fraction of trials that females chose X_1 over X_2 , which are given by the entries of Table 1. We also calculated the likelihood for these estimates using equation (1) but we replaced $p_i/(p_i + p_j)$ by $n_{ij}/(n_{ij} + n_{ji})$. If the relative preference model adequately described the data, we expected that the increase in likelihood gained by the more flexible unconstrained choice model would not be significant. The likelihood ratio is an appropriate test statistic (Mendenhall et al. 1986). The relative preference model had eight free parameters, and the unconstrained choice model had 36, so the unconstrained choice model had 28 more degrees of freedom. Twice the logarithm of the ratio of the

likelihoods of the two models was 49.34, which was significant at the 0.01 level for a chi-square distribution with 28 degrees of freedom.

Thus, we rejected the relative choice model because the unconstrained model fit the data significantly better. This result is particularly striking because the relative choice function is so widely used in models of sexual selection and mate choice.

Since we could reject the first two choice functions, we considered a third hypothesis that we call the ‘absolute with error choice function’. As the name suggests, it is based on the notion of error (Phelps et al. 2006). The idea is that each stimulus elicits an initial preference value, but then an error term is added to arrive at the final preference value. This error could result from the perceptual system of the female, or from experimental sources. The focal stimulus is chosen if its final preference value is larger than that of the competing stimulus. Phelps et al. (2006) proposed using a normally distributed error term. The choice function is then

$$C(X_1, X_2) = \int_{-\infty}^{\infty} f(\epsilon_2) \int_{p(X_2) - p(X_1) + \epsilon_2}^{\infty} f(\epsilon_1) d\epsilon_1 d\epsilon_2, \quad (2)$$

where $f()$ is the density of a standard normal distribution with variance σ_ϵ^2 .

We estimated the preferences for the nine stimuli in Table 1 and the error variance σ_ϵ^2 using the maximum likelihood method described earlier. The estimated preferences are shown in Table 2. They differed, in some cases substantially, from the estimates based on relative choice.

Table 2. Preference estimates for female túngara frogs*

	Sc	Sb	Ob	Oa	Oc	Sa	Sd	Od	M
Relative	1	1.03	1.53	1.65	2.14	2.30	3.38	4.04	4.37
Error	1	1.02	1.38	1.44	1.67	1.74	2.08	2.24	2.31

*Maximum likelihood estimates of female preferences for the nine stimuli in Table 1. Relative: estimates under the relative choice function; Error: estimates under the absolute with error choice function. The two-letter codes refer to stimuli described by Ryan & Rand (2003).

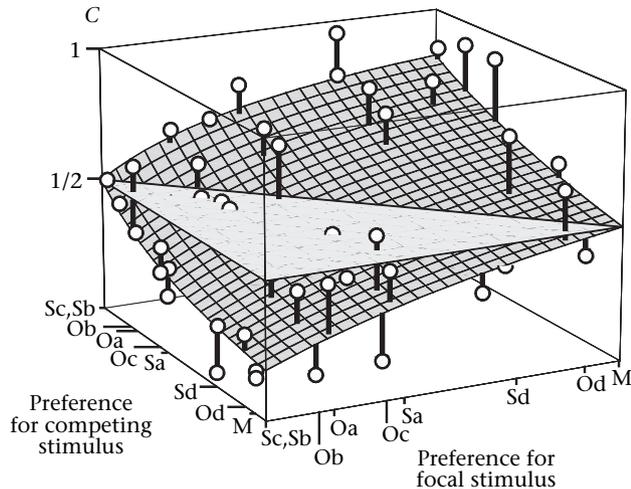


Figure 5. The relative choice function (gridded surface) and the fraction of choices made by female túngara frogs (shown as lollipops) based on the data in Table 1. The grey horizontal plane shows equal preferences for the two stimuli ($C = 1/2$). Estimates for each of the nine stimuli (as indicated by their positions on the horizontal axis) were estimated by maximum likelihood (Table 2). The preference values on the two horizontal axes range from 1 to 4.4. The two-letter codes refer to stimuli described in detail by Ryan & Rand (2003).

This result illustrates the general point that the value of a preference can only be interpreted in the context of a specific model for choice. We tested the goodness of fit of the absolute with error choice function by again comparing its likelihood with that of the unconstrained model. The results were significant at the 0.01 level, allowing us to reject the model.

Although we rejected three plausible (and widely used) choice functions that obeyed strict preference, these negative results provided no guidance as to whether the data might be adequately described by some other choice function consistent with strict preference. Therefore, we considered a possibility at the other extreme, that túngara frogs do not have strict preferences but instead show intransitive choice.

Do Frogs Show Intransitive Mate Choice?

If choice is not based on strict preferences, then intransitive choice is possible. We can look for evidence of intransitivity without making specific assumptions about the rules governing choice.

The idea here is to look for sets of stimuli such that females choose X_1 over X_2 , X_2 over X_3 , and X_3 over X_1 . Recall that intransitivity involving more than three stimuli implies that there must be an intransitivity among three of them. An intransitive cycle of three stimuli might be obscured by sampling error, however, so a conservative approach is to look for intransitivities involving any number of stimuli.

It is difficult to draw conclusions just by inspecting the data matrix. Table 1 shows four pairs of stimuli whose response trials do not follow a simple ranking, suggesting

there is a possibility for intransitivity but not demonstrating it. We therefore make use of a simple method from graph theory. Begin with the 'adjacency matrix' in which element a_{ij} equals 1 if there are more responses to stimulus i than j (that is, $n_{ij} > n_{ji}$) and is 0 otherwise. If there is a cycle of length k somewhere in the matrix, then a 1 will appear along the diagonal when this matrix is raised to the k th power (Rosen 1999, page 472).

We applied this algorithm to the data in Table 1. No cycles of any length ($3 \leq k \leq 9$) were found. Thus, we found no evidence for intransitivity. Of course, this finding does not rule out that possibility. Intransitivities that are present between the stimuli could be obscured by sampling error, or intransitivities might appear with other stimuli that were not tested.

The results of our analyses of mate choice in túngara frogs are ambiguous. On the one hand, we can firmly reject three strict preference models. On the other hand, there is no support for intransitive choices among the stimuli that were tested. Túngara frogs may use strict preference functions other than those that we tested, or they may not use preferences at all. Given appropriate combinations of stimuli, túngara frogs might even show intransitive choice. While the results of our analyses leave us frustrated in our understanding of this species, they do show clearly that our basic assumptions about mate choice need to be reevaluated. Furthermore, the statistical methods developed here provide tools that may be useful in other studies of mate choice.

DISCUSSION

Even in the simple setting of binary trials, simple choice rules can produce complex outcomes, including intransitive choice. This possibility has been implicitly precluded in virtually all studies of mate choice, both theoretical and empirical. The implicit assumption has been that choice is based on strict preference. By that we mean that a female assigns a univariate preference to each male, independent of other males, and that the probability that she chooses a male increases with the strength of this preference. This appears to be the first study of mate choice to have tested that hypothesis. The fact that we cannot find support for strict preference suggests that the basic rules of mate choice in animals warrant closer study.

Several studies have estimated mating preference functions with respect to a single stimulus parameter, such as call frequency. These studies either use no-choice trials or compare female responsiveness to test stimuli in binary trials with a single reference stimulus (e.g. Ritchie 1996; Basolo 1998; Gerhardt et al. 2000; Shaw & Herlihy 2000). In essence, these studies estimate a one-dimensional slice through the choice function with a fixed competing stimulus. This approach could be extended by using the same procedure with other competing stimuli. If these (univariate) preference functions are not strictly proportional to each other, we would reject the proportional choice model for strict preferences. Murphy & Gerhardt (2000) collected data that could be analysed in this way, but the analysis that they performed nevertheless

assumes implicitly that females use strict preference. In summary, many studies have assumed strict preference, but we are not aware of any other study that has tested that assumption.

There are several possible explanations for why we were not able to find a model of choice consistent with strict preference. The first two models assume that females show strict preference. We rejected the three most widely assumed choice functions, all consistent with strict preference, but perhaps females follow another rule that we did not test. A second possibility is that the females that we used in the choice trials individually used strict preference, but they differed in their preferences. Variation among females in choice behaviour is well documented (Jennions & Petrie 1997). The females that we tested could have differed in their internal state (e.g. hormone levels). Female response to mating stimuli in this species is affected by oestrogen levels (Lynch et al. 2006). Our statistical approach did not account for between-female variation, and perhaps that is the reason that the choice functions that we considered were rejected.

A different set of hypotheses suggest that mate choice in túngara frogs does not obey strict preference. One possibility here is that a female's internal representation of her response to a stimulus cannot be summarized by a single preference score (a violation of Criterion 1). A second possibility is that a female does score each stimulus, but that increasing values of this score do not always make her more likely to choose that stimulus (a violation of Criterion 2).

We have focused here on binary choice for two reasons: its simplicity makes it a good place to start analysis and it is widely used as an experimental paradigm. Obviously, there are many settings in which females choose between more than two alternatives. A number of our results carry over to those situations. In particular, strict preference as defined by Criterion 1 and Criterion 2 still gives sufficient conditions to guarantee that choice will be transitive. Interesting outcomes are possible if mate choice between three or more males is not based on strict preference.

For example, females might show context-dependent choice that depends on the set of males present. That is, a female's internal representation of a particular male may depend not only on that male, but also on the other males present. This effect would violate the first and perhaps also second criterion for strict preference. The addition of an unpreferred alternative can cause humans to change their relative rankings of two preferred options (Tversky & Simonson 1993). Starting with work on honeybees (Shafir 1994), foraging studies have repeatedly demonstrated context-dependent choice behaviour that depends on the range of alternatives present (Hurly & Oseen 1999; Waite 2001; Bateson 2002a, b, 2004; Bateson et al. 2002; Shafir et al. 2002). Those workers have emphasized the importance of assimilating more complex decision rules into the choice paradigms used in studies of animal behaviour.

Context-dependent choice can, of course, be triggered by factors other than the stimuli being compared. While choice studies in the laboratory seek to control for many of those variables, females in nature are confronted by

a large number of irrelevant stimuli. The other sounds, or the auditory scene, from which a call must be parsed, for example, can influence the perception of that signal (Bregman 1990). Similarly, the audience of other receivers can influence the animal's perception of a signal (Otter & Ratcliffe 2005), with mate choice copying being just one example of such a phenomenon (Matos & Schlupp 2005). Yet another situation not captured by simple mate choice rules is when female behaviour changes with experience.

Our interest in strict preference is largely motivated by the question of whether mate choice is transitive or not. We did not find support for intransitivity, but that negative result certainly does not rule it out. It is possible that the test stimuli that we used evoked intransitive choice but the effect was masked because of sampling noise. Alternatively, there may be other stimuli that we did not test that would produce intransitive choice.

If mating preferences should turn out to be intransitive, a fascinating series of evolutionary possibilities would emerge. One can imagine scenarios in which intransitive choice could cause cycling evolution of male display traits (Maynard Smith 1982, page 19; Sinervo & Lively 1996). This scenario in turn could lead to divergence between populations in those displays, even in the absence of differences in the choice rules that females use. Under some conditions, intransitive choice could also maintain polymorphism for male displays within a population.

Despite the great interest in mating behaviour, we have almost no understanding of the basic features of the rules that females use to choose mates. The results from this study suggest that those rules are more subtle than has been previously assumed. More work is needed to illuminate those rules and to determine their consequences.

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Appendix

Here we show conditions that are sufficient for intransitivity in binary choice. First, we observe that a set of more than three stimuli that show intransitive choice implies that there is a subset of only three of them that also show intransitivity. To see this, consider a set of four stimuli that show the intransitive relation $X_4 \Rightarrow X_3 \Rightarrow X_2 \Rightarrow X_1 \Rightarrow X_4$. Here we use $X_i \Rightarrow X_j$ as shorthand to mean that stimulus X_i is chosen over X_j more often than not. We can have either $X_4 \Rightarrow X_2$ or $X_2 \Rightarrow X_4$, and either $X_3 \Rightarrow X_1$ or $X_1 \Rightarrow X_3$. Enumerating the four combinations of these possibilities shows that there is always a set of three stimuli among the original set of four that shows intransitivity. The argument generalizes immediately to sets with more than four stimuli. Thus, we can reduce an intransitive relation involving any number of stimuli to a problem involving only three of them.

Our next goal is to show what intransitivity implies about the geometry of the choice function. We make the restrictive assumptions that the choice function is a piecewise continuous function, and that the effects of any stimulus can be reduced to a single parameter s . Take three stimuli X_1 , X_2 and X_3 , ordered in increasing value of this parameter: $s_1 < s_2 < s_3$. For intransitivity, either $X_3 \Rightarrow X_2 \Rightarrow X_1 \Rightarrow X_3$, or $X_3 \Rightarrow X_2 \Rightarrow X_1 \Rightarrow X_3$. Assume the first case for concreteness; the argument extends directly to the second case. Then qualitatively the three couplets of points fall in regions of the choice function

C as shown on the right side of Fig. 3: two of the couplets correspond to positive values of C and one to a negative value. By a continuity argument, this implies that there is at least one pair of stimuli with values r_1 and r_2 such that $C(r_1, r_2) = 1/2$, $s_1 > r_1 > s_2$ and $s_2 > r_2 > s_3$. A second continuity argument then leads to Condition 2 for strong stochastic intransitivity discussed in the text.

The geometry of the choice function corresponding to this situation is shown in Fig. 3. An example of a pair of stimulus values that meet the condition just developed is indicated by the open circles.