

Measuring female mating preferences

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Abstract. Interest in the evolution of female mating preferences has increased greatly in recent years, and numerous hypotheses have been proposed to explain how mating preferences evolve. Despite this interest, little is known about how selection acts on mating preferences in natural populations. One reason for this lack of information may be that experimental designs commonly used for testing female preferences make it difficult to quantify the preferences of individual females. Most commonly used designs share three features: they examine the preferences of populations of females, they test female responses when they are presented simultaneously with two stimuli, and they infer information on female preferences by observing female choices between alternative stimuli. Population-level choice tests, in which each female is tested only once with a set of stimuli, do not evaluate within-female variation in preference, which is necessary to document between-female variation in preference. Two-stimulus designs test only for directional preferences if female responses are tested with only a single pair of stimuli. In addition, dichotomous scoring of female responses makes detection of between-female variation in preference difficult. Simultaneous stimulus presentations can confound female preference and female sampling behaviour. An alternative method to assess female preferences is to measure repeatedly the preference functions of individual females using a single-stimulus design. The shape of a female's preference function indicates how a female's mating response varies with male trait value, and repeated measures of individual preference functions allow measurement of within- and between-female variation in preferences.

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Darwin (1871) was the first to propose that female mating preferences can result in selection on male morphology and behaviour. Since then, particularly over the last two decades, many studies have confirmed that females prefer some trait variants over others and that males with preferred traits have enhanced mating success (reviewed by Thornhill & Alcock 1983; Searcy & Andersson 1986; Kirkpatrick 1987a; Andersson 1994). Sexual selection by female choice can therefore be important in the evolution of male secondary sexual traits. More recently, attention has focused on the factors that influence the evolution of female preferences (reviewed in Bradbury & Andersson 1987; Kirkpatrick & Ryan 1991; Andersson 1994).

Three general experimental approaches have been adopted to study the evolution of female mating preferences. First, a comparative approach

can be used to examine historical associations between male traits, female preferences, and environmental factors (Hamilton & Zuk 1982; Read & Harvey 1989; Basolo 1990a; Hill 1994; Ryan & Rand 1995). For example, statistical associations across populations between preferences and traits have been used to evaluate whether female preferences and male traits have coevolved (Houde & Endler 1990; Hill 1994; Morris et al. 1996). Second, the benefits of an average preference of a population of females can be examined. For example, in populations where females tend to prefer one trait variant over another, the potential benefits of this preference have been evaluated by examining the fitness consequence of mating with males with different trait values (Burley 1981; Grant & Grant 1987; Rutowski et al. 1987; Yosef & Pinshow 1989; Knapp & Kovach 1991). Third, selection on mating preferences can be measured directly by assessing the relationship between the strength of a preference and female fecundity and survivorship.

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For some questions about the evolution of female preferences, a comparative approach is the most appropriate method (Basolo 1990a; Ryan & Rand 1990, 1995; Proctor 1992). When examining the adaptive significance of female preferences, however, historical associations between female preferences and other variables are merely suggestive; such correlations can arise because of causal relationships or because the preference and the other variable of interest are both correlated with some other variable (Houde 1993; Frumhoff & Reeve 1994). In contrast, examinations of the adaptive significance of population-level preferences can help to determine whether selection currently acts on mating preferences. There are, however, at least two important drawbacks with this approach. First, there may be adaptive variation in female preferences; some females might benefit from having preferences different from the population average (e.g. Potts et al. 1991). Under such circumstances, examining the benefits of population-level preferences may lead to a misleading view of the factors influencing the evolution of female preferences. Second, selection on female preferences is likely to be multifactorial; more than one direct source of selection is likely to act on female preferences, and indirect selection can act on female preferences due to phenotypic correlations with other traits under selection. As a result, the examination of a single benefit of a population-level preference may provide an incomplete view of the factors influencing the evolution of female preferences.

An alternative approach is to measure how selection acts on mating preferences within natural populations. Such studies would allow us to assess the fitness consequences of variation in female preferences, the relative importance of different sources of selection, and whether correlations with other traits result in indirect selection on female preferences. For example, we could assess the relative importance of direct selection on preferences due to variation in survivorship and fecundity and indirect selection on preferences due to variation in offspring viability. Almost no studies have attempted to assess how selection acts on mating preferences within natural populations. Current selection on a preference does not necessarily mean that the preference has evolved because of that source of selection. Without an understanding of how selection currently acts on female preferences, however, understand-

ing the general process of preference evolution will be difficult.

To understand selection on a female preference, we need to know the form of individual preferences (for example, are individual preferences stabilizing or directional), the nature of variation between females in the preference, the fitness consequences of preference variation, and patterns of phenotypic correlation between the preference and other traits under selection, including other preferences. To understand the evolution of a female preference, we also need to know the extent of additive genetic variation for the preference and patterns of genetic correlation between the preference and other traits with fitness consequences. Little is known about the form of female preferences (but see Gerhardt 1991; Basolo 1995; Wagner et al. 1995), about between-female variation in preferences (but see Sappington & Taylor 1990; Ryan et al. 1992; Møller 1994; Wagner et al. 1995), or about phenotypic correlations between preferences (but see Wagner et al. 1995). Even less is known about phenotypic correlations between female preferences and other traits in females. Similarly, little is known about genetic variation in female preferences (but see Majerus et al. 1982; Bakker 1993; Wilkinson & Reillo 1994), and almost nothing is known about genetic correlations between female preferences and other female traits, including genetic correlations between different preferences. Thus, attempts to explain the evolution of female preferences have been made with only a rudimentary understanding about the nature of the trait of interest.

In this paper I argue that current methods for assessing female preferences may sometimes be inadequate if our aim is to understand how selection acts on female preferences rather than how female preferences result in selection on male traits. In fact, the dearth of studies examining selection on mating preferences in natural populations may be partially attributable to current methodology. To examine selection on mating preferences, it is necessary to have a quantitative measure of the strength of a female's mating response to different trait variants. Many designs commonly used to assess female preferences make it difficult to obtain such information accurately. First, I discuss the difference between mate choice and mating preference. Because common experimental designs examine mate choices, and because choices are outcomes that are determined

by multiple factors, only one of which is preference, it is important to address why these terms should not be used synonymously. Second, I review common experimental designs used to assess female preferences, and I discuss some of their limitations. Third, I make recommendations for future experimental designs. Specifically, I discuss the value of obtaining repeated measures of the preference functions of individual females, and how preference functions can be derived.

MATE CHOICE, PREFERENCE AND SAMPLING BEHAVIOUR

The terms choice and preference are often either used synonymously in studies of sexual selection, or the relationship between the two is not made explicit. This synonymization of choice and preference is evident in the use of choice tests to assess female preferences; we observe female mating decisions and make inferences about female preferences. Because our assay of preference is female choice, the two are operationally synonymous. It is important, however, to distinguish between female choices and female preferences because choices can be affected by factors independent of preferences.

Heisler et al. (1987) defined female choice as differential mating by females as a result of mating preferences. This definition recognizes that mate choice is an outcome, and that this outcome results, at least in part, from an internal property of females, mating preferences. Preferences affect the responses of females to males based on the expression of male traits, and preferences thus affect female mating decisions. However, mate choices can be affected by other internal properties of females. Because females have a limited time in which to mate, because of such factors as environmental constraints on the timing of reproduction and predation risks associated with searching, females usually cannot sample all males within a population. Selection should thus favour sampling strategies by females that represent a balance between the benefits obtained by finding a preferred mate and the costs associated with increased sampling. Sampling strategies can potentially take a number of forms (see Parker 1978; Janetos 1980; Dombrowsky & Perrin 1994; Wiegmann et al. 1996). Female sampling strategies have been examined in detail for few species

(but see Trail & Adams 1989; Bensch & Hasselquist 1992; Dale et al. 1992), but the effect of female sampling strategies on mate choice should be obvious. Consider an animal in which females differ in the number of males they sample but do not differ in their preferences. Females that sample many males before mating will show a greater bias in their mate choices than females that sample only a few males before mating. Sampling strategies can thus affect female mate choices independently of female preferences. Female sampling behaviour may be a direct consequence of female preferences, as assumed by some models of preference evolution (e.g. Kirkpatrick 1987b; Pomiankowski 1987), or preference and sampling behaviour may be separate traits that vary independently of each other. No data are currently available to assess these alternatives.

Female choices can also be modified by environmental factors that do not affect either the nature and strength of female preferences or the nature of female sampling behaviour. For example, the mate choices made by female frogs in a complex acoustic environment can be affected by the difficulty of discriminating between simultaneous, overlapping calls (Gerhardt & Klump 1988; Forrest 1994). Thus, females with identical preferences and sampling strategies might differ in their mate choices depending on environmental conditions at the time they make their choices.

Given that female mate choices can be influenced by mating preferences, sampling strategies, environmental conditions and perhaps other factors, female choice seems best defined as differential mating by females as a result of the interaction of environmental conditions, mating preferences and sampling strategies. This paper will focus on the study of female preferences, an area with a substantial body of literature and an established experimental protocol. It could be argued that because selection results from the fitness consequences of female mate choices, it is mate choice that we should be concerned about. However, as discussed above, choice is an outcome of preference and other factors. To understand the evolution of mating preferences, we need to study preferences per se. To understand fully female mating decisions, however, and thus to understand fully sexual selection by female choice, it is important to understand not only female preferences, but also both female sampling

strategies and the manner in which environmental conditions affect the ability of females to discriminate between male traits.

COMMON CHOICE DESIGNS

Most standard methods used to test whether females discriminate between potential mates based on variation in a male trait share three common features. First, they are population-level preference tests. The preferences of a number of females from a population are each tested once with a set of stimuli, and the investigator statistically evaluates the hypothesis that the population of females studied prefers one trait value over another. Second, they are two-stimulus tests. Females are presented with two stimuli, often trait variants from opposite extremes of the trait frequency distribution. Third, they are simultaneous stimulus presentations. Stimuli are presented to females at the same time. Methods can vary depending upon the type of animal studied and the investigator conducting the work. The responses of females can be scored dichotomously (yes or no for each stimulus within a stimulus pair) or on a continuous scale (for example, the time spent in courtship with each stimulus within a stimulus pair). Examples of some typical experimental designs are presented below. I have included examples from the work of myself and collaborators whenever possible.

In anuran amphibians and orthopteran insects, acoustic signals produced by males often play a central role in mate choice; males call to attract females, and females discriminate between potential mates to a large degree based on the structure of male calling behaviour (e.g. Whitney & Krebs 1975; Popov & Shuvalov 1977; Ryan 1980; Hedrick 1986; Simmons 1988). A standard method of testing female preferences in these animals is the two-speaker choice test (e.g. Gerhardt 1974; Popov & Shuvalov 1977; Ryan 1980; Sullivan 1983; Wagner 1996). A receptive female is placed equidistant between two speakers. Synthetic calls differing in only one parameter (for example, repetition rate or duration) are broadcast from each speaker. The female is observed until she contacts one of the speakers, at which time a choice is considered to have occurred. A number of females are tested, the number selecting each stimulus is tallied, and a binomial or chi-square test is used to test the null

hypothesis of no difference in response. If females show a significant bias towards one of the stimuli, it is concluded that females prefer greater (or lesser) values of the parameter manipulated.

In many fish, visual signals appear to play an important role in mate choice; males differ in their courtship behaviour, body size, ornament size and coloration, and females discriminate between potential mates based in part on variation in these traits (e.g. Semler 1971; Farr 1980; Houde 1987). A standard method of testing female preferences in these animals is also the two-stimulus choice test (e.g. Hemens 1966; Ryan & Wagner 1987; Basolo 1990b; Milinski & Bakker 1990; Rowland et al. 1995). An aquarium is generally divided into three or more sections, with the end sections sealed off from the centre section(s) by glass or Plexiglas. Males differing in one or more traits are placed in the end sections and a female is placed in a removable compartment in the centre of the tank. After an acclimation period the compartment around the female is removed. The time the female spends in sections near each male, or the time the female spends in courtship with each male, is recorded. A number of females are tested, all with the same pair of males or each with a different pair of males, and the null hypothesis of no difference in response to males with different trait values is statistically evaluated. If females show a significant bias towards one of the males, it is concluded that females prefer the trait value characterizing the preferred male. Some investigators have used modified choice designs (e.g. Houde 1987), and some have used models and video images rather than live males (Rowland 1989; Rowland et al. 1995), but the basic methodology is similar.

In birds, both acoustic and visual signals play important roles in mate choice; males differ in their songs and morphology, and females discriminate between males based in part on variation in these traits (Andersson 1982; Catchpole et al. 1984; Burley & Coopersmith 1987; Searcy 1994). To examine female preferences based on male morphology or song structure, females are generally placed in an arena either with live males differing in morphology, with models differing in morphology, or with speakers broadcasting different song types (e.g. Burley et al. 1982; Hill 1990; Zuk et al. 1990; Collins 1995; Mateos & Carranza 1995). The number of stimuli presented to females is often between two and four, and the females may or may not be able to come into physical

contact with either the test males or artificial stimuli during the tests. The time females spend in association with each stimulus or the number of mating displays given to each stimulus is recorded, and the null hypothesis of no difference in female response is tested. If females show a significant bias towards one of the stimuli, it is concluded that females show a preference, either based on the manipulated trait or based on the trait that varies between the live males. Some researchers have examined female responses to alternative stimuli in the field (e.g. Mountjoy & Lemon 1996), but the methodology is essentially the same.

METHODOLOGICAL LIMITATIONS

Two of the primary advantages of the types of choice designs discussed above is that they are easy to conduct and that the results are easy to analyse and interpret. In addition, they have proved to be invaluable in documenting population-level mating preferences. These types of experimental designs, however, may sometimes provide either a misleading or an inadequate representation of female preferences. First, they tend to mask potential variation in preferences between females. Second, they can mistakenly result in the conclusion that a trait is unimportant to females. Third, they sometimes allow evaluation only of directional preferences. Fourth, these designs evaluate female preferences by observing mate choices; because mate choices are affected by factors other than mating preferences, they can provide misleading information about the strength of female preferences. Some studies have attempted to assess female preferences by observing female mate choices under natural conditions (reviewed by Andersson 1994). Such studies not only suffer from some of the above problems, but they also suffer from an inability to discriminate between the effects of female preference and male–male competition on female mate choices. Even though males may not fight directly over females, competition for territories or advertisement sites may affect which males are available for females to sample, and thus may affect the types of males with which females mate.

Limitations of Population-level Preference Tests

For some questions, we wish to know simply whether biased male mating success with respect

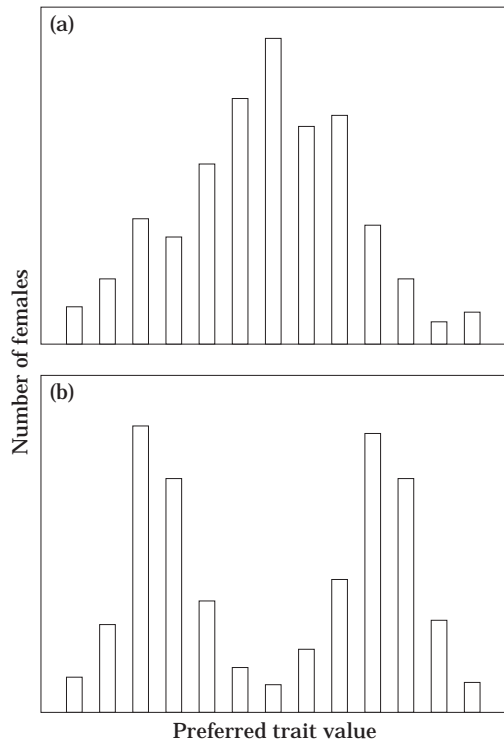


Figure 1. Hypothetical distributions of female preferences within a population. In both examples there is variation between females in their preferences. (a) Continuous variation in female preferences, with the preferences of individual females distributed around some mean trait value. (b) Discontinuous variation in female preferences, with some females preferring low trait values and some females preferring high trait values.

to a particular trait could be due to female choice based on the trait. For example, we may measure directional sexual selection on male coloration in a bird and want to know whether female preferences are at least partially responsible for this pattern. For such questions, population-level preference tests may be adequate. However, negative results cannot be used to suggest that the trait is unimportant to females. Aside from the problem of accepting the null hypothesis of no preference, individual females may have preferences, but the direction of preferences may differ among females (e.g. Fig. 1; Wagner et al. 1995). If some females prefer higher trait values but other females prefer lower trait values, population-level preference tests may mistakenly suggest that females do not discriminate between males based on the trait.

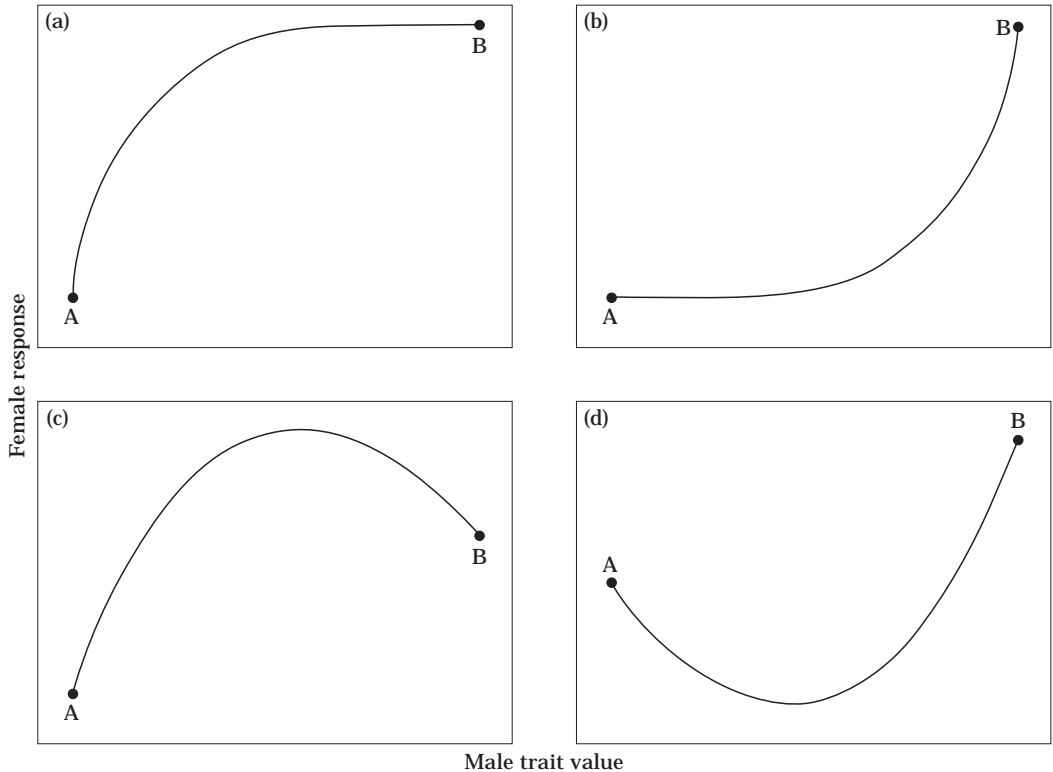


Figure 2. Hypothetical preferences of individual females. Despite substantial differences in the forms of the preferences, in all cases females would prefer trait value B to trait value A.

A more important limitation of population-level preference tests is that they provide no information about between-female variation in preferences. Because each female is tested only once with any set of stimuli, and because repeated measures of a trait are necessary to determine whether the trait varies between individuals (unless the trait is invariant within individuals), it is impossible to derive information about between-female variation from population-level choice tests. If we want to examine selection on female mating preferences, we first need to measure the preferences of individual females, which requires repeated testing of individuals with the same stimuli (e.g. Godin & Dugatkin 1995; Wagner et al. 1995; Gerhardt et al. 1996).

Limitations of Two-stimulus Choice Designs

Two-stimulus choice designs commonly compare female responses to trait values from the

extremes of the trait frequency distribution. When such tests use only a single pair of stimuli to assess female responses, they can severely limit the types of hypotheses that can be tested about the structure of a preference. When one extreme is favoured over another, a directional preference is usually inferred (e.g. Wagner & Sullivan 1995). Even when one or both trait values fall near the average of the trait frequency distribution, a preference for one value over another often leads to an inference of directionality. If preferences are stabilizing or disruptive, however, a single set of two-stimulus tests will not permit detection of such non-directional preferences (Fig. 2; see also Gerhardt 1991). In numerous studies of sexual selection, female responses have been compared only to extremes from the male trait distribution. The results of two-stimulus choice tests may have led investigators to attribute observed patterns of directional sexual selection to the presence of directional female preferences when

female preferences were actually stabilizing or disruptive.

Through the use of multiple stimulus sets, it is possible to detect stabilizing or directional preferences with a combination of two-stimulus presentations. For example, Gerhardt (1991) presented male calls differing in pulse rate and dominant frequency to female grey treefrogs, *Hyla versicolor*. By testing the extreme trait values against intermediate trait values, he demonstrated that population-level preferences based on these traits were stabilizing. In contrast, when male calls differing in duration were presented to females in a similar manner, females always preferred greater trait values. Such experiments are an advance over tests in which female responses to only two extremes are tested. In relatively few studies have a variety of trait values been tested against each other in a two-stimulus choice design.

Dichotomous Scoring of Female Responses

Two-stimulus choice tests can be a problem when female responses are scored dichotomously, because dichotomous data can obscure between-female variation in preferences. Dichotomous choice tests in which females are scored as preferring either one stimulus or its alternative, are common with certain groups, such as crickets and frogs (Popov & Shuvalov 1977; Ryan 1980; Wagner & Sullivan 1995; Wagner 1996). If females differ in the direction of their preferences (i.e. some females prefer high trait values and others prefer low trait values), dichotomously scored two-stimulus choice tests may allow the division of females into groups that consistently prefer one extreme, those that consistently prefer the other extreme, and those that show no preference. If females differ in the strength of their preferences but not in the direction of their preferences, however (i.e. all females prefer the same extreme but differ in how strongly one extreme is preferred over another), two-stimulus choice tests may have insufficient resolution to demonstrate such variation unless many tests are conducted with each stimulus pair (see below). For example, between-female variation in a cricket preference was not detected using a two-stimulus choice design (Ritchie 1992), but was detected in a different species of cricket using another design (Wagner et al. 1995).

Dichotomous scoring of female responses can also be inefficient. Suppose we want to assess the form of an individual female's preference. If we test each female four times with a pair of stimuli, female responses can be divided into five character states: 4-0, 3-1, 2-2, 1-3, 0-4. To assess adequately the form of each female's preference, each female needs to be tested with several-stimulus sets that vary in the degree of difference between the contrasted stimuli. If we use five-stimulus sets, the preferences of each female will need to be measured 20 times (five sets, four tests with each set). Next, suppose we want to assess within- and between-female variation in the preference. Each female's preferences will need to be re-tested with each set of stimuli at a different time. Repeating the set of tests results in a total of 40 tests of each female. In contrast, if we had a continuous measure of female response, each female's response to the five sets of stimuli could be tested once, and then females could be re-tested with each set of stimuli at a different time. Rather than 40 tests of each female, we would need only 10 tests (five sets, one test with each set, two repetitions of these tests). As a result, dichotomous scoring of female responses greatly increases the number of tests that must be conducted with each female. Although inefficient, it is possible using a dichotomous choice design to examine both the form of an individual female's preference and variation between females in their preferences.

Limitations of Simultaneous Stimulus Presentations

Simultaneous stimulus presentations can potentially confound measures of female preferences. As discussed above, mate choice is the outcome of female preferences and female sampling behaviour. Because simultaneous stimulus presentations allow immediate comparisons between traits, and because the outcome of this comparison may be a choice between the alternatives, such tests can make female preferences appear stronger than they actually are. Also, because simultaneous stimulus presentations provide females with the opportunity to examine their alternatives repeatedly, differences between females or taxa in their sampling behaviour can be misinterpreted as differences in preference. These criticisms are discussed below.

Choice tests in general can result in an amplification of female preferences (Wagner et al. 1995). Consider two traits, *a* and *b*, that differ by a small but perceivable amount. Females might respond strongly to both when the traits are presented singly, but show a slightly stronger response to trait *b*. When the two traits are presented simultaneously to females, however, and females are therefore presented with a choice, they might choose the more preferred trait and therefore respond much more strongly to trait *b* than to trait *a*. Because preferences are inferred by observing female choices, we may mistakenly infer that a trait is more strongly preferred than it is.

Choice tests can also compromise comparisons of preferences between individuals, between populations and between taxa because of variation in female sampling behaviour. Consider two females (or taxa) that have identical preferences. Female A repeatedly samples males before making a choice and female B samples each male once before making a choice. The behaviour of these females may differ in a simultaneous stimulus presentation. Female A may spend more time than female B in proximity or courtship with the less preferred male due to repeated sampling, making it appear that the strength of her preference is weaker than that of female B. Because female sampling behaviour can affect how females respond to alternative stimuli in simultaneous choice tests, it may be difficult to make conclusions about variation between females or between taxa from such designs, unless female sampling behaviour is either invariant or predictably correlated with preference. This is much less of a problem when preferences are inferred from female choices between two stimuli than when preferences are inferred from female association or courtship behaviour. Differences in female sampling behaviour should not affect which of two stimuli a female ultimately selects, but they may affect the relative time spent in association with each stimulus and the relative number of courtship displays given to each stimulus.

QUANTITATIVE MEASURES OF FEMALE PREFERENCES

Describing Female Preferences

The information we want about female preferences depends on the question we want to address.

At the simplest level, we might wish to know whether an observed pattern of directional sexual selection on a male trait can be explained, in part, by a female preference based on that trait. In such cases, we want to know whether, at the population level, female preferences show a directional bias. No information about the nature of between- and within-female variation is usually necessary, and we may or may not need to know the detailed structure of female preferences. Simultaneous, two-stimulus choice tests in which the preference of each female is tested only once are useful under such conditions, particularly if females are tested with multiple pairs of stimuli (e.g. Gerhardt 1991). Such methods have proved to be very successful in demonstrating that females have mating preferences, and that these preferences result in sexual selection on male traits. If we want to characterize the preferences of individual females, however, these methods may be inadequate.

A complete description of female preferences has three requirements. First, either a continuous or multinomial measure of female responses to male trait variants is necessary. Unless female responses can be divided into multiple character states, assessing either the form of female preferences or the extent of variation between females in their preferences will be difficult. Second, it is necessary to measure female responses to a number of individual stimuli or sets of stimuli. Without the presentation of a series of stimuli to individual females, assessing the form of female preferences will be impossible. Third, it is necessary to test females repeatedly with each stimulus or set of stimuli. Without repeated testing of females, assessing the extent of between-female variation in preferences is impossible.

Given that we want our measures of female preferences to satisfy the above requirements, a useful method of describing female preferences is the determination of preference functions, where the preference functions of individual females are measured on at least two occasions (for example, on different days). A preference function describes how the strength of a female's mating response to a male trait varies with the degree of expression of the trait (Fig. 2). Preference functions are a common feature of genetic models of the evolution of preferences (e.g. Lande 1981; Kirkpatrick 1982; Heisler 1985), and preference functions can potentially be measured for individual females as well as for populations of females. This type of data has

the advantage of providing a nearly complete characterization of the form of female preferences, allows comparison of the extent of variation in a preference between and within females, and allows comparison of preferences between populations.

Few studies have described the preference functions of individual females (but see Wagner et al. 1995). To compare variation in the strength of a female's response to variation in the expression of a male trait, the responses of individual females to multiple stimuli or stimulus sets must be tested. Some have argued that preference functions will be impossible to obtain for most animals, because testing individual females against a range of male trait values is not feasible (e.g. Heisler 1994). In many of the animal systems commonly used to study female mating preferences, however, it is possible to test individual females repeatedly (e.g. Godin & Dugatkin 1995; Wagner et al. 1995; Gerhardt et al. 1996). The dearth of information on female preference functions may have more to do with the familiarity of established methodology, which make preference function estimates difficult to obtain, than with the inability to test individual females repeatedly.

A more important problem with deriving female preference functions is that they require an assay that allows female responses to be categorized into a number of states. For some animals, such as anuran amphibians, such measures may be difficult to obtain. Such an assay is possible, however, using a large number of dichotomous choice tests. Experimental ingenuity may also make such measures possible (e.g. Doherty & Pires 1987). For other groups of animals, female mating responses can be measured in some obvious ways, including the number of copulation solicitations given in response to different stimuli (Zuk et al. 1990), the number of courtship displays given in response to different stimuli (Mateos & Carranza 1995), the time spent in association or in courtship with different stimuli (Burley et al. 1982; Basolo 1995; Rowland et al. 1995) and the amount of movement towards different stimuli (Doherty & Pires 1987; Wagner et al. 1995).

Measuring Female Preference Functions

Given that it is possible to test individual females repeatedly, and given that we have a measure of female response that allows multiple

character states, we can measure female preference functions in two ways. First, we can measure relative female preference functions. A relative preference function describes the strength of a female's mating response to trait variants relative to other trait variants. Second, we can measure absolute female preference functions, which describe the strength of a female's mating response to trait variants presented by themselves. Each of these types of preference functions are discussed below.

Relative preference functions

A relative preference function describes variation in the strength of a female's response with variation in difference values between two male traits. For example, we might measure the time a female fish spends in association with each of two stimuli in a two-stimulus choice design, where individual females are tested with multiple pairs of stimuli, each of which varies in the degree of difference in the male trait of interest. We could then examine the correlation between the difference in the time spent with the two stimuli and the difference in trait value. For example, Basolo (1990b) presented female swordtail fish, *Xiphophorus helleri*, with a choice between males that differed in sword length. Females spent more time with the male that had the longer sword; the greater the difference between the males in sword length, the greater was the relative time the female spent with the male that had the longer sword. These results suggest that a female's response to a male is positively correlated with male sword length.

Two general types of relative preference functions are: standard and variable relative preference functions. These two types of relative preference functions differ in the types of stimuli females are asked to choose between.

A standard relative preference function compares the variation in the relative response of females to two stimuli and the variation in the difference values between the two male stimuli, where one of the stimuli is held constant between tests while the second varies relative to this standard. For example, relative female preference functions might be examined based on male body size, where an average body size stimulus is tested against multiple smaller and larger body size stimuli. In such a test, the difference in female

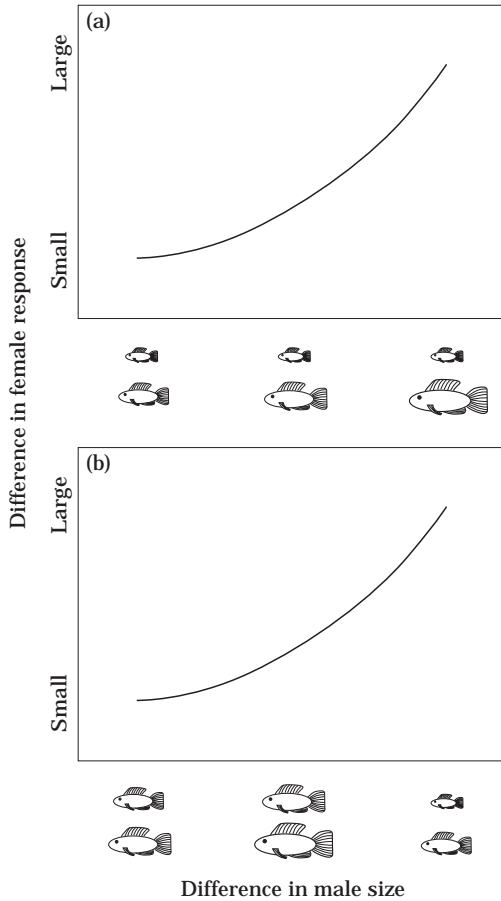


Figure 3. Hypothetical relative preference functions based on male size. (a) Standard relative preference function. (b) Variable relative preference function. See text for an explanation of these different measures of preference function. As the difference between males increases in a series of paired stimulus presentations, female mating response to the larger male in the pair increases.

courtship time might be measured with stimuli of 20 cm versus 40 cm, 30 cm versus 40 cm, 50 cm versus 40 cm, and 60 cm versus 40 cm (Fig. 3a).

A variable relative preference function compares the variation in the relative response of females to two stimuli and the variation in the difference values between the two male stimuli, where none of the stimuli are held constant between tests. For example, relative female preference functions might be examined based on male body size, where the body size stimuli presented to females vary not only in their difference

values, but also in their absolute values. In such a test, the difference in female courtship time might be measured with stimuli of 50 cm versus 60 cm, 60 cm versus 80 cm, and 20 cm versus 50 cm (Fig. 3b).

One important advantage of relative preference function tests is that they can be used to derive preference functions for species where it is difficult to detect differences in female responsiveness to stimuli presented singly. For example, females of some species may not show differences in their responses to different male traits unless they are allowed a comparison between stimuli with different trait values. The disadvantage of relative preference function tests is that they suffer the same problem as other types of simultaneous stimulus presentations: they can confound female preferences and female sampling behaviour.

Of the two types of relative preference function tests, the variable relative preference function tests may be preferable, if the absolute stimulus values used in the different comparisons are randomized. By randomizing the absolute stimulus values used in the difference comparisons, we may derive a more general preference function. Consider the consequence of measuring standard relative preference functions when female preference functions are non-linear. For example, females may discriminate between two smaller males that differ in body size by 10 mm, but they may not discriminate between two larger males that differ in body size by 10 mm. Under such conditions, the relative preference function we derive will depend upon whether the standard stimulus is a small male or a large male. Because different standard trait values can produce different relative preference functions, standard relative preference functions may provide a less general measure of female preference.

Absolute preference functions

An absolute preference function describes variation in the strength of a female's response to a stimulus with variation in stimulus value, where each stimulus is presented individually to females (e.g. Basolo 1995; Wagner et al. 1995). For example, we might measure female responses to males of different body size, where males of different size are presented sequentially to females (Fig. 4). The relationship between female mating response and male trait value could then be examined.

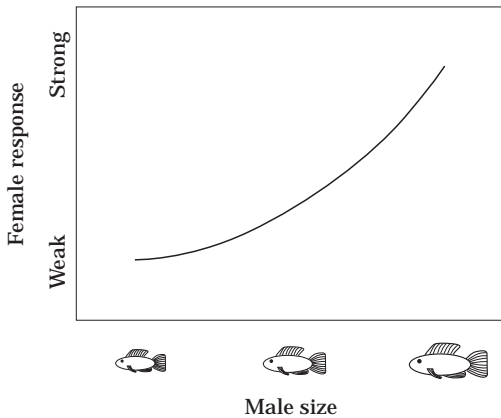


Figure 4. Hypothetical absolute preference function based on male size. As male size increases in a series of sequential presentations, female mating response increases.

For many animals, the determination of female preference functions requires only a simple modification of the two-stimulus design. Rather than placing two stimuli on opposite sides of an enclosure, one stimulus can be placed in one end compartment and either no stimulus or a female in the opposite compartment. Female responses to a series of sequentially presented stimuli can then be measured, and preference functions can be derived by examining the relationship between female response and stimulus trait value (e.g. Basolo 1995). For birds, the time spent in association or the number of mating displays given to sequentially presented stimuli can be used to derive female preference functions. For acoustic orthopteran insects and, potentially, anuran amphibians, the amount of movement towards sequentially presented stimuli can be used to assess the strength of a female's mating response (e.g. Doherty & Pires 1987; Wagner et al. 1995). Branham & Greenfield (1996) presented population-level preference functions for two traits in a firefly using a single-stimulus design; individual preference functions could be similarly derived.

Limitations of Sequential Stimulus Presentations

There are some potential limitations of using sequential stimulus presentations to assess female preferences. First, females of some species either may not respond to stimuli presented in isolation

or may not show differences in their responses to sequentially presented traits. Some species show strong differences in response to traits presented either sequentially or in isolation (Doherty & Pires 1987; Basolo 1995; Wagner et al. 1995; Branham & Greenfield 1996), but there may be some taxa for which such tests are impractical. For species that will not respond to sequential stimulus presentations, however, the measurement of relative rather than absolute preference functions should be possible. Second, the results of sequential stimulus presentations may not accurately predict female mate choices. This is a problem that needs to be explored. No one has yet compared the preference functions of individual females and the responses of the same females in a simultaneous choice test to determine whether the two types of tests give consistent results. Until more information is available about female responses in the two types of preference tests, it may be necessary to validate the sequential stimulus approach for each species studied. Third, individual females may differ in their responsiveness to traits presented in isolation. Thus, females with identical preferences may differ in their assessed preferences. For such differences to confound measures of female preference functions, however, they must affect the slope or shape of the preference function, not just the Y-intercept. Fourth, a female's responsiveness to a stimulus in a sequential stimulus presentation may be affected by the stimuli to which she has already been presented. This problem can be minimized by randomizing the order in which stimuli are presented and by statistically controlling for residual order effects. This is also a problem when multiple two-stimulus choice tests are conducted using the same female over a short time.

CONCLUSION

Some of the most important insights in behavioural ecology have arisen from the recognition that both between- and within-individual variation in behaviour can be adaptive. In contrast, research on the evolution of female mating preferences has usually focused on population-level analyses of female behaviour. In some studies, phenotypic and genetic variation in female preferences have been shown, and in a few, within-female changes in mating preferences associated

with changes in environmental or internal conditions have been shown (Forsgren 1992; Hedrick & Dill 1992; see also Berglund 1992). Little attention has been devoted to the possibility that selection may favour alternative preference phenotypes within a population, or that plasticity in female preferences may be favoured by selection. To understand how selection acts on mating preferences, a much better understanding is needed of the trait we are attempting to explain.

I have argued that commonly used methods may sometimes be inadequate to assess both the form of female preferences and within- and between-female variation in preferences. Most importantly, the use of simultaneous stimulus presentations confounds sampling behaviour and mating preferences. If we are interested in the factors that influence the evolution of female preferences, we need to measure preferences *per se*, not an outcome of preferences that is also affected by sampling behaviour and environmental conditions. Sequential rather than simultaneous stimulus presentations may reduce this problem, especially in studies that use time in association with a male to assess female response.

I have also argued that repeated measures of female preference functions allow us to obtain the information about female preferences needed to examine selection on preferences. First, preference functions provide more complete information about the form of female preferences than it is possible to obtain from typical choice tests. Second, it is possible to identify alternative preference phenotypes by comparing within- and between-female variation in preference functions. Other methods may also provide this information, and each investigator needs to find a suitable method for their system that allows quantitative measures of the strength of individual female preferences. Without assays that provide accurate information about both the form of female preferences and the nature of variation within and between females in preferences, it will be difficult to understand how selection acts on preferences, and thus why preferences evolve.

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