

VARIATION IN MATE CHOICE AND MATING PREFERENCES: A REVIEW OF CAUSES AND CONSEQUENCES

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ABSTRACT

The aim of this review is to consider variation in mating preferences among females. We define mating preferences as the sensory and behavioural properties that influence the propensity of individuals to mate with certain phenotypes. Two properties of mating preferences can be distinguished: (1) ‘preference functions’ – the order with which an individual ranks prospective mates and (2) ‘choosiness’ – the effort an individual is prepared to invest in mate assessment. Patterns of mate choices can be altered by changing the costs of choosiness without altering the preference function. We discuss why it is important to study variation in female mating behaviour and identify five main areas of interest: Variation in mating preferences and costs of choosiness could (1) influence the rate and direction of evolution by sexual selection, (2) provide information about the evolutionary history of female preferences, (3) help explain inter-specific differences in the evolution of secondary sexual characteristics, (4) provide information about the level of benefits gained from mate choice, (5) provide information about the underlying mechanisms of mate choice. Variation in mate choice could be due to variability in preference functions, degree of choosiness, or both, and may arise due to genetic differences, developmental trajectories or proximate environmental factors. We review the evidence for genetic variation from genetic studies of heritability and also from data on the repeatability of mate-choice decisions (which can provide information about the upper limits to heritability). There can be problems in interpreting patterns of mate choice in terms of variation in mating preferences and we illustrate two main points. First, some factors can lead to mate choice patterns that mimic heritable variation in preferences and secondly other factors may obscure heritable preferences. These factors are divided into three overlapping classes, environmental, social and the effect of the female phenotype. The environmental factors discussed include predation risk and the costs of sampling; the social factors discussed include the effect of male–male interactions as well as female competition. We review the literature which presents data on how females sample males and discuss the number of cues females use. We conclude that sexual-selection studies have paid far less attention to variation among females than to variation among males, and that there is still much to learn about how females choose males and why different females make different choices. We suggest a number of possible lines for future research.

Key words: Female mate choice, mate preferences, mating decisions, variation, sexual selection, mate sampling, female–female competition.

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I. INTRODUCTION

(1) *Historic background*

The evolution of extravagant secondary sexual characters ('ornaments') has been the subject of intense theoretical and empirical investigation (Andersson, 1994). However, in spite of the enormous amount of work conducted, a few issues have dominated to the exclusion of others. Initially, Darwin's claim that female choice played a role in the evolution of male secondary sexual characters was doubted (Cronin, 1991). Early research therefore aimed at demonstrating this phenomenon by looking at male mating success. Was variation in male mating success non-random? If so, could it be related to differences in male traits? Numerous correlational and experimental studies from many taxa now confirm that males with increased ornamentation, or possessing certain attributes, have a mating advantage arising from female mate choice (reviews: Bradbury & Andersson, 1987; Ryan & Keddy-Hector, 1992; Andersson, 1994; Møller, 1994a; Johnstone, 1995).

Subsequent research then concentrated on determining what selection pressures could maintain seemingly costly female mating preferences. Three main explanations have been proposed: (1) preferences may be directly selected due to direct benefits which increase female survival or fecundity (Reynolds & Gross, 1990); (2) preferences may be maintained by indirect selection due to genetic benefits that increase offspring fitness. Two types of genetic benefits are recognized. Choice may lead either to the production of offspring with genotypes that increase viability ('good genes' or 'viability

genes'), and/or to the production of sons with genotypes that make them more attractive (Fisherian traits) (reviews: Kirkpatrick & Ryan, 1991; Andersson, 1994); (3) preferences may be maintained as pleiotropic effects of natural selection on female sensory systems in contexts other than mate choice, such as foraging or predator evasion (Enquist & Arak, 1993; Ryan, 1994; Arak & Enquist, 1995). If benefits gained outside the context of mating outweigh the cost of preferences during mate choice, net selection will maintain preferences (Christy, 1995). However, if the mating preference is costly, there may be selection for modifiers that alter sensory functioning or processing during mate choice, thereby altering the preference (Christy & Backwell, 1995).

Despite interest in the question of what maintains *female* preferences, most work has focused on *male* traits. First, significant heritability of preferred male traits has been documented (Hedrick, 1988; Hill, 1991; Norris, 1993; Pomiankowski & Møller, 1995). Second, several studies indicate that preferred males sire offspring with higher viability or fecundity (e.g. Reynolds & Gross, 1992; Norris, 1993; Petrie, 1994). Thus, a current question of great interest is how ornaments honestly signal 'genetic' quality. This has led to renewed interest in the handicap principle (Zahavi, 1977; Grafen, 1990), and has encouraged research into the costs of ornamentation (Evans & Thomas, 1992; Balmford, Thomas & Jones, 1993*a*; Borgia, 1993; Jennions, 1993; Møller & de Lope, 1995). There have also been several attempts to correlate degree of ornamentation with possible indices of male 'quality' (Møller & Pomiankowski, 1993*a, b*; for a detailed review see Johnstone, 1995).

Much attention has been given to the often larger amounts of phenotypic variation in the size of male ornaments compared with other morphological traits (Alatalo, Höglund & Lundberg, 1988*b*; Barnard, 1994). One popular explanation for this trend is that variation in male quality determines the costs incurred with increased investment in ornaments, leading to condition-dependent expression of sexual traits in accordance with the handicap principle of signalling (Grafen, 1990). In contrast, few researchers attempt to account for variation in female mating preferences in terms of differing costs and benefits. Males appear to trade-off the benefits of larger ornaments against the increased costs of developing and maintaining them (Møller & de Lope, 1995). Likewise, we might also expect females to trade-off the benefits gained from being choosy against the costs of stronger preferences. Moreover, because of differences in age, experience, body condition and size, we might also expect that these trade-offs will differ among females (Höglund & Alatalo, 1995). Variation in female quality should determine the point at which investment in mate choice is optimized, leading to condition-dependent expression of preferences. Although we now know something about the benefits of mate choice for both direct (e.g. Hill, 1991) and indirect benefits (e.g. Norris, 1993; Petrie, 1994), we know almost nothing about the costs. Do different preference functions carry different costs? Does sampling increase the risk of predation or disease transfer? How much time and energy is invested into sampling males? What tactics can females use to reduce the potential costs of sampling?

Recently, it has been suggested that a typological view prevails in which female mating preferences are seen as species-specific, stereotypic traits (W. Eberhard & W. Wcislo, in preparation). It is claimed that the implicit view is along the lines of 'in species X, females prefer to mate with males with larger ornaments, and this preference is reflected in the pattern of mate choice'. With a few notable exceptions, there has been

little research into: phenotypic variation in mating preferences; female sampling tactics; analysis of constraints on optimal mate choice; variation among individuals in their mate-choice decisions; or consideration of the consequences of this variability for evolution by sexual selection. In this article, we aim to consider why it is important to study variation in female mating behaviour, and then to review our current understanding of possible causes.

(2) *Definitions*

Following Heisler *et al.* (1987), we define 'mating preferences' as the sensory and behavioural properties that influence the propensity of individuals to mate with certain phenotypes. 'Mate choice' is then defined as the pattern of mating which arises, in part, because of these mating preferences. We further subdivide 'mating preferences' because there are two properties that can be distinguished conceptually and, more importantly, sometimes empirically. We define 'preference functions' as the order in which an individual ranks prospective mates *ceteris paribus*; and 'choosiness' as the effort or energy that an individual is prepared to invest in assessing mates, both in terms of the number of mates sampled and the amount of time spent examining each mate. Increased choosiness could arise by changes in sampling tactics, or by a higher mating threshold. We believe the distinction between preference function and choosiness is useful. The pattern of mate choice can be altered by changing the costs of female choosiness with no apparent change in terms of which a male a female would most prefer to mate with (i.e. an unchanged preference function) (e.g. Milinski & Bakker, 1992; Hedrick & Dill, 1993; Backwell & Passmore, in press). Our subdivision also accords with common usage: '*prefer* implies preconceived partiality for one thing over another but does not always connote the actual getting of what one *chooses*' (Webster's Dictionary).

II. WHY STUDY VARIABILITY IN FEMALE MATING PREFERENCES AND MATE CHOICE?

There are many reasons why variability in female preferences is worth studying. Here, we provide an incomplete list, mentioning five areas of research which we find particularly interesting.

First, variation in mating preferences and costs of choosiness influences the rate and direction of evolution by sexual selection. Increased variability in preferences which affects the mean level of a preference will decrease the intensity of female-driven directional selection on male ornaments, as well as subsequent indirect selection on the preference itself. Changes in the frequency distribution of mating preference functions may also lead to shifts in the net direction of selection and, in some cases, disruptive selection may even occur, leading to speciation (Turner & Burrows, 1995). In contrast, a sampling tactic such as mate copying increases the advantages of common male traits, making it more difficult for novel traits to evolve (Kirkpatrick & Dugatkin, 1994). Costs to choosiness also decrease the intensity of sexual selection. Gomulkiewicz (1991) modelled the effect of limited female choice by adjusting the average number of males that females sampled. Decreased sampling made it more difficult for novel male traits to evolve. When there is individual variation in susceptibility to costs, however, this may cause shifts in the direction of selection. For example, consider a species where

some females prefer shorter-tailed males and others longer-tailed males. If constraints on choosiness differ between the two types of females and vary over time or space, or are subject to frequency-dependent selection, fluctuations in the direction of selection will result.

A key variable in recent models of the evolution of multiple male sexual traits is the cost of mating preferences. For Fisherian traits, increased costs (greater than the additive cost of each individual preference) may still lead to the evolution of multiple preferences (Pomiankowski & Iwasa, 1993). However, for traits indicating viability, only a preference for a single trait is stable if assessment of additional traits increases costs disproportionately (Iwasa & Pomiankowski, 1994). Similarly, a model which predicts continual changes in mating preferences and repeated evolution of male traits assumes that stronger preferences carry greater costs (Iwasa & Pomiankowski, 1995). In addition, the model only predicts repeated evolution of new preferences when the correlation between trait and preference exceeds a threshold value. This value is strongly influenced by the intensity of stabilizing natural selection on the preference. Kirkpatrick & Barton (1995) suggest that the threshold is unlikely to be reached under natural conditions. Moreover, the effect of variation in female quality has not even been incorporated into these models. Clearly, however, the usefulness of these models depends crucially on quantitative data on the costs of mate choice. How strong is stabilizing natural selection on preferences? Is a preference for larger male ornaments more costly? Do costs increase disproportionately when females assess several male traits?

Second, variability in mating preferences provides information on their evolutionary history. Specifically, Fisherian evolution of ornaments predicts considerable heritable variation in female mating preferences, both within and between populations (Lande, 1981). At present, there is comparatively little information on the heritability or coefficient of additive genetic variation (cf. Pomiankowski & Møller, 1995) of mating preferences (but see Bakker & Pomiankowski, 1995). Knowledge of genetic differences between populations may also provide data on differences in selection regimes between areas and the extent to which preferences are subject to natural selection (but see Houde, 1993). The genetic basis of female preferences may also provide some insight into the speciation process. Turner & Burrows (1995) suggested that the genetic bases of preferences may lead to different speciation rates among lineages. In contrast to Fisherian models, female choice for males with 'viability genes' requires neither genotypic nor phenotypic variation among females (e.g. Grafen, 1990); although polygenic models obviously assume a heritable basis to preferences, and generally predict coevolution of preference and preferred trait (Bakker, 1993).

Regardless of whether Fisherian or viability-gene processes operate, a positive genetic correlation between preference and male trait indicates that these traits have coevolved. Sensory exploitation is often presented as the main alternative to models requiring genetic coevolution (Ryan, 1994). Current phylogenetic tests of sensory exploitation are based on female preferences remaining stable through speciation events (Ryan, 1994; Shaw, 1995). The implicit suggestion is that a single, invariant female preference shared by ancestral and derived species can be characterized (Christy & Backwell, 1995). However, if there is population variability in female preferences, stability not only requires that the mean preference remains the same, but also that the

frequency distribution of preference functions *and* choosiness in the population is unchanged. At present, evidence for stability is based on data that the mean preference function at the population level is unchanged (e.g. Ryan *et al.*, 1990). However, selection on female choosiness could lead to very different patterns of mate choice. For example, two species could both have auditory tuning curves with identical best excitatory frequencies. The effective mating preferences will be very different, however, if females in one species sample several males, while in the other they mate with the first male encountered.

Third, it may be possible to explain inter-specific differences in the evolution of secondary sexual characters by relating different tactics of mate choice to ecological, social or morphological factors. To date, most attempts to explain variation in ornamentation among species invoke strong natural selection against the elaboration of male traits (e.g. Balmford *et al.*, 1993 *a*; Winquist & Lemon, 1994). However, both the potential for females to be choosy and variability in preference functions may be equally important predictors of differences in male ornamentation. Factors that inhibit female choice will reduce selection for elaborate male traits. Variation in the opportunity for mate choice may also affect other features of mating behaviour. For example, Slagsvold *et al.* (1988) suggest that polygyny in pied flycatchers (*Ficedula hypoleuca*) is partly due to high female sampling costs leading to limited searches for unpaired males. (For a general discussion of the costs of choosiness see Noë & Hammerstein, 1994.) Sullivan (1994) has also noted that, given severe time constraints on female choice, females are likely to use static morphological traits that are quickly assessed. When more time is available, choice may be based on behavioural displays which take longer to perform. Hence, information on the duration over which females assess males may explain some inter-specific variation in male ornamentation.

The psychophysics of female choice may also explain some variation in male ornamentation. Cohen (1984) has noted that Weber's 'law' provides an inevitable constraint on male ornamentation. This 'law' summarizes a general finding from psychology that the ability of an individual to discriminate a fixed size difference between stimuli decreases as the absolute size of the stimuli increases. It may therefore be more difficult for females to distinguish between males as the size of ornaments increases, reducing the benefits of choosiness. Furthermore, the ability to distinguish between stimuli may vary among taxa and different stimuli (e.g. acoustic *versus* visual) which could also generate inter-specific differences. Theoretical models often make assumptions about female discriminatory abilities, which need to be tested. For example, Iwasa & Pomiankowski (1995) state that 'small ornaments are worse indicators of male viability because differences in size are more difficult to distinguish'. However, Weber's law suggests that the function relating efficiency as an indicator to signal size is more likely to be a parabola than a continually increasing function.

Fourth, given phenotypic plasticity in female mating preferences, it is possible to manipulate the costs of choosiness and examine the effect on mate choice. This should provide information about the benefits associated with discriminatory mating. For example, if benefits are small, we should be able to detect cost-reducing changes in female sampling behaviour. Experimentally, costs can often be precisely controlled, and the benefits conferred by choosing can then be assessed by titrating known costs against unknown benefits. It is intriguing, for example, that a cost to a female as

seemingly small as swimming against a water current can lead to a reduction in mating success for redder bellied male three-spined sticklebacks (*Gasterosteus aculeatus*) (Milinski & Bakker, 1992). This implies that the benefits of mating with redder males are fairly small, even if male redness does signal some aspect of male quality (Milinski & Bakker, 1990).

Fifth, once the importance of variability in female mating preferences is recognized, a more mechanistic account of mate choice should emerge. Only when traits show variability can one look for correlations which eventually facilitate causal explanations. Other areas in behavioural ecology have benefited greatly by integrating functional and mechanistic approaches (Real, 1994). Among-female variability should provide information on the neurobiology and psychology of female choice (W. Eberhard & W. Wcislo, in preparation), and the interaction between sensory systems and ecological conditions. As Ryan (1994) has noted, knowledge of mechanisms provides a stronger base when explaining why certain traits have evolved (e.g. Haines & Gould, 1994). In the same way that researchers have been challenged to explain variability in male ornamentation, they will also need to account for variability among females. There is now evidence that the interaction between female condition and investment in sensory apparatus, or time and energy allocated to mate choice, provides part of the explanation (see Section VIII). In general, we are missing valuable opportunities to explain variation in data, which is presently dismissed as 'statistical noise'. Empirical data takes time to collect, and should be used as fully as possible. For example, in two-choice mating experiments, statistical analysis is often limited to binomial tests determining whether there is a significant preference for a trait at the population level. But why do some females choose the 'non-preferred' trait? Numerous explanations exist but these are rarely explored. Females may simply make mistakes (Wiley, 1994), vary in their receptivity (Rowland *et al.*, 1995), their ability to discriminate stimuli (Cohen, 1984; Gerhardt, 1987), their choosiness or in their preference functions. For example, Jennions, Backwell & Passmore (1994), Polakow *et al.* (1995) and Ryan, Perrill & Wilczynski (1992) found that female body size explained some variation in choice in phonotaxis experiments using frog calls that differed in spectral frequencies. In the cricket frog *Acris crepitans*, body size appears to be related to preference functions, while in the reed frog *Hyperolius marmoratus* it may influence the ability of females to distinguish stimuli.

III. EXPLAINING VARIATION IN MATE-CHOICE DECISIONS

When a group of females are presented with the same choice of mates, not all females choose to mate with the same male. For example, in lekking species, mating is not confined to a single 'preferred' male (reviewed by Balmford, 1991; Wiley, 1991; Höglund & Alatalo, 1995). Why? An obvious source of variation in mate choice is that females vary in their mating preferences. This could be due to variability in preference functions, degree of choosiness, or both. This variation may arise due to genetic differences, developmental trajectories, or proximate environmental factors.

Heritable variation among individuals is the raw material necessary if evolution is to occur. It is therefore crucial that we understand why there is variability in mating preferences. Our aim in this review is to highlight possible causes of variability, and to consider the consequences for evolution by sexual selection. Reflecting our interests as

field biologists, we have tried to provide real-life examples, and ideas that can be empirically tested. A genuine gap in our knowledge exists, but one which is amenable to investigation.

IV. GENETIC VARIATION IN MATING PREFERENCES

Most theoretical models of the evolution of female choice assume a heritable genetic basis to mating preferences (e.g. Fisher, 1930; Lande, 1981; Iwasa, Pomiankowski & Nee, 1991). Studies which demonstrate heritable variation are thus central to their validation (Boake, 1989; Bakker, 1990; Ritchie, 1992*a*). At equilibrium in the Fisherian process, and in most polygenic models of 'viability gene' sexual selection, theory predicts positive genetic covariance between the mating preference and male ornament (Bakker, 1993; Breden, Gerhardt & Butlin, 1994; Pomiankowski & Sheridan, 1994). Evidence for genetic variation in mating preferences has recently been reviewed in detail by Butlin (1994) and Bakker & Pomiankowski (1995). Here, we provide a brief review of evidence obtained from controlled breeding experiments (selection studies or lineage analysis) and examination of discrete genetic analyses. We then focus in detail on the use of data on repeatability of mate choice. In many species, breeding experiments are impossible but repeated testing of mate choice can provide information on the upper limits to heritability. Perhaps more interestingly, it also increases the likelihood of detecting relationships between mate-choice decisions and contingent environmental or phenotypic factors.

(1) *Genetic studies of heritability*

Several experiments have tested for heritable mating preferences by selecting for specific mating preferences. In one of the first studies by Majerus, O'Donald & Weir (1982), female two-spotted ladybird (*Adalia bipunctata*) that mated with melanistic males were selected for each generation. The population showed a significant increase in the proportion of females mating with melanistic males, indicating a heritable basis to mating preferences. Moreover, the pattern of mate choice was consistent with variation in this mating preference being due to only one or a few genes (Majerus *et al.*, 1986). Unfortunately, recent work shows that the interpretation of these results is less clear cut (reviewed by Ritchie, 1992*a*). Attempts to repeat the earlier experiments and select for mating preferences for melanistic males, both from wild stock and from lineages from earlier experiments, failed (Kearns *et al.*, 1992). O'Donald & Majerus (1992) have highlighted some potential problems with the study of Kearns *et al.* (1992) and also present some new data which are suggestive of a genetic basis to the preference. Other selection studies have also revealed additive genetic variation in mating preferences in a range of species [guppies, *Poecilia reticulata* (Houde, 1994; but see Breden & Hornaday, 1994); stalk-eyed flies, *Cyrtodiopsis dalmanni* (Wilkinson & Reillo, 1994); fruitflies, *Drosophila melanogaster* (e.g. Crossley, 1974; Kaneshiro, 1989), *D. mercatorum* (Ikeda & Mauro, 1982), *D. mojavensis* (Koepfer, 1987); bollworms, *Pectinophora gossypiella* (references in Collins & Cardé, 1990); planthoppers, *Ribautodelphax imitans* (De Winter, 1992); and grasshoppers, *Chorthippus brunneus* (Charalambous, Butlin & Hewitt, 1994)]. In these studies, the mating preference was either directly selected for, or the preferred trait was selected for and the preference changed as a correlated response (see Bakker & Pomiankowski, 1995).

Discrete genetic effects are associated with different mating preferences in several species. In the sulphur butterfly *Colias eurytheme*, there are two female colour morphs which differ in their choice of mates. Female coloration is heritable (Sappington & Taylor, 1990). Tebb & Thoday (1956) found that female fruitflies, *D. melanogaster*, differing in genotype (heterozygote *versus* the two homozygotes) preferred different male genotypes. Similarly, Heisler (1984) presented evidence for a genetic basis to female mating preferences for wild-type and yellow mutant males in *D. melanogaster*. In seaweed flies *Coelopa frigida*, different female preferences are associated with different inversion karyotypes (Gilburn, Foster & Day, 1993; Gilburn & Day, 1994) and different alleles at the alcohol dehydrogenase locus (Engelhard, Foster & Day, 1989). Some breeding studies using lineage analysis (e.g. father–daughter, full-sib/half-sib design) also suggest a genetic basis to preferences. This has been shown by father–daughter analysis of a pheromone-based mating preference in the cockroach *Nauphoetia cinerea* (Moore, 1989). This finding is interesting as pheromones appear to signal dominance and active choice of dominant males leads to both indirect and direct benefits (Moore, 1994). This begs the question why all females do not prefer dominant males to the same extent? Father-son analysis in a moth (*Argyrotaenia velutinana*) also indicates a heritable male mating preference for female pheromones (Roelofs *et al.*, 1986). In brown planthoppers (*Nilaparvata lugens*), work on repeatability of female responses to male acoustic signals showed differences between isofemale lines suggestive of a genetic basis. However, the variation in female responses was in the ‘preference window’ (range of stimuli responded to), not in the mean preference (Butlin, 1993). Of course, not all studies of the underlying basis of variation in preferences reveal a genetic component. For example, Johnson *et al.* (1993) found no evidence from mother–daughter analysis for heritable mating preferences in red junglefowl (*Gallus gallus*). Likewise, Nicoletto (1995) found no heritable female mating preference for amount of male orange coloration in guppies (*P. reticulata*). In a review, Ritchie (1992a) also cited two unpublished studies in which selection for female preferences was unsuccessful (see also Boake, 1989; Ritchie, 1992b). As always, the possibility that negative results are less likely to be published should be considered.

Bakker (1993), using a full-sib/half-sib breeding design, reported a genetic basis to female preferences for male redness in three-spined stickleback (*G. aculeatus*). Moreover, there was also a positive genetic correlation between male colouration and female preference. Father–daughter analysis also suggested a positive genetic correlation between preference and preferred trait in the cockroach, *N. cinerea* (Moore, 1989, 1990) and the redbanded leafroller moth, *A. velutinana* (Roelofs *et al.*, 1986). Several recent studies have applied artificial directional selection for preferred traits and recorded correlated changes in preferences. When these changes are in the same direction as that of the selection on the male trait, this indicates a positive genetic correlation [stalk-eyed fly, *C. dalmanni* (Wilkinson & Reillo, 1994); guppy, *P. reticulata* (Houde, 1994; but see Breden & Hornaday, 1994); fruitfly, *D. mercatorum* (Ikeda & Mauro, 1982); bollworms, *P. gossypiella* (several studies, see Collins & Cardé, 1990); planthopper, *R. imitans* (De Winter, 1992); and the grasshopper, *C. brunneus* (Charalambous *et al.*, 1994)]. These results are intriguing, because some theoretical models suggest that genetic correlations are unlikely to be maintained by non-random mating unless effective population size is very large (Nichols & Butlin, 1989; see

Gilburn & Day, 1994). For a general critique of these studies see Breden *et al.* (1994) and Pomiankowski & Sheridan (1994).

Studies looking at differences between populations can also provide information on the genetics of mating preferences. For example, research on guppies (*P. reticulata*) (Houde, 1988; Houde & Endler, 1990; Endler & Houde, 1995; cf. Nicoletto, 1995) and grasshoppers (*Ephippiger ephippiger*) (Ritchie, 1991) both show heritable variation in mating preferences. In cricket frogs (*A. crepitans*), differences among populations in female auditory tuning curves exist. These are independent of mean population body size, although other environmental factors that differ between populations cannot be excluded (Ryan & Wilczynski, 1988; Ryan *et al.*, 1992). Demonstrating a genetic basis to preferences does not, however, address the difficult question of the maintenance of within-population variation. There are also difficulties in accounting for differences among populations in terms of the main models for the evolution of female preferences (see Houde, 1993). However, the apparent absence of among-population variation (at least as characterized by 'mean preferences'), despite variation in preferred male traits, suggest that there are adaptive or genetic constraints on the evolution of preferences and/or ornaments (Ryan & Wagner, 1987; Ryan *et al.*, 1990). Constraints on preference evolution are consistent with some sensory exploitation models for the evolution of male ornaments (Shaw, 1995; but see Christy, 1995; Christy & Backwell, 1995).

(2) *Repeatability as an indicator of heritability*

With large, long-lived animals, the practicality of performing breeding experiments is daunting (but see Johnson *et al.*, 1993). In these species, investigating the repeatability of mate choice (whether or not individuals make the same choice when reassessing the same potential mates) offers another approach to the study of variation (Boake, 1989; Gerhardt, 1992). Repeatability provides an index of the level of phenotypic variation among females and sets an upper limit to heritability. For example, if females do not show repeatable mate-choice decisions, there is presumably no variation in mating preferences among females (but see below). Observed variation in mate choice can therefore be attributed to within-individual variation or stochastic events. Conversely, repeatable patterns of mate choice that vary among females suggest individual differences in mating preferences.

Few experimental studies of mate-choice repeatability have been performed. Gerhardt (1974) found that nine out of 12 female treefrogs (*Hyla cinerea*) chose the same stimulus in at least 75 % of tests, when offered a choice between a conspecific and hybrid call. Robertson (1986) noted that when female red-groined toadlets (*Uperolia laevigata*) were experimentally separated from their mate and then released back into the chorus they tended to remate with the same male. Møller (1994b) reported repeatable female mate choice for male tail length in the barn swallow (*Hirundo rustica*), and Godin & Dugatkin (1995) found repeatable female choice for amount of orange colouration in guppies (*P. reticulata*). Wagner, Murray & Cade (1995) also reported repeatable female responses with respect to some parameters of advertisement calls in field crickets (*Gryllus integer*). In a two-choice laboratory experiment, Poulin (1994) also found that bullies (*Gobiomorphus breviceps*) preferentially chose to mate with the male they first visited.

In contrast, Ritchie (1992b) did not find repeatable female preferences for calls

varying in syllable number within a population of bushcrickets (*E. ephippiger*), and Boake (1989) found no repeatability of female choice based on pheromones in a mealworm beetle (*Tenebrio castaneum*). Perhaps the most interesting negative result is that of Ligon & Zwartjes (1995a). They offered female red junglefowl (*G. gallus*) five successive opportunities to choose between two males. In their initial choice, 13 out of 15 females chose a male with a large ornamental head comb; but in the subsequent four trials only four of the females mated exclusively with the large-combed male. Thus, while the females appeared to be able to discriminate between males, most of them actively chose to mate with both males. There is now evidence that females sometimes mate multiply to generate sperm competition (e.g. Madsen *et al.*, 1992), and the implications of this for Fisherian and 'viability gene' models for mating preferences for males with large ornaments have yet to be fully explored. Superficially, there is a contradiction between the claim that females choose males with large ornaments because this indicates possession of 'good genes' and the claim that females mate with a variety of males (including males with small ornaments) because this improves offspring viability. Olsson & Madsen (1995) suggest that multiple mating in lizards may occur because males do not possess phenotypic traits that are reliable indicators of genetic quality. Females may therefore promote sperm competition as the only way in which to obtain sperm from high-quality males. In contrast, Stockley *et al.* (1994) suggest that multiple mating in common shrews, *Sorex araneus*, is a mechanism to reduce the risk of inbreeding. The extent to which these different explanations are applicable may vary across taxa (Petrie & Jennions, in press).

While individual repeatability of mate choice is a prerequisite for heritable genetic variation in preferences (but see Butlin, 1993), repeatability may also be due to non-heritable factors. Jennions *et al.* (1994) reported repeatable phonotactic responses in a frog (*H. marmoratus*). However, this did not appear to be due to variation in preference functions, but rather a size-based ability of females to discriminate between signals. Similarly, in the frogs *U. laevigata* and *Ololygon rubra* there is very strong assortative mating with respect to body size (Robertson, 1986, 1990; Bourne, 1993), suggesting that repeatability of mate choice for different-sized males is due to variation in female size. If body size is a consequence of food availability during ontogeny rather than genetic variation (e.g. Emlen, 1994), there will be non-heritable, but repeatable, female preferences for different-sized males. On the other hand, if female body size has a heritable component, this effectively represents a source of genetic variation in mating preferences.

In some cases, epigenetic factors mimic genetic heritability, even when breeding experiments are performed. ten Cate & Bateson (1988, 1989) have noted that sexual imprinting in birds may lead to preferences for conspicuous male characters that are inherited. A preference for novel mates combined with an asymmetry in response may lead to a preference for 'supernormal stimuli' (see Bakker, 1990). For example, a female sexually imprinting on her father who is long-tailed may preferentially mate with slightly longer-tailed males. In turn, her daughters, because their father is long-tailed, will also show a preference for longer-tailed males. A significant argument has also been proposed in terms of the 'peak-shift' effect, whereby learning to discriminate between negative and positive stimuli leads to stronger responses to stimuli of a greater magnitude than the initially preferred stimulus (Weary, Guilford & Weisman, 1993).

In several birds, females tend to remate with the same male either within or across seasons [e.g. cock-of-the-rock *Rupicola rupicola* (Trail & Adams, 1989); white-bearded manakin *Manacus manacus* (Lill, 1974); golden-headed manakin *Pipra erythrocephala* (Lill, 1976); Lawes' parotia *Parotia lawesii* (Pruett-Jones & Pruett-Jones, 1990); and black grouse *Tetrao tetrix* (Rintamäki *et al.*, 1995)]. In general, learning the identity of males and then remating with a familiar male may also explain some cases of repeatability of mate choice.

An important methodological issue not addressed in previous studies of repeatability is that variation in female receptivity or motivation can alter estimates of repeatability (see Rowland *et al.*, 1995). They found that female sticklebacks (*Gasterosteus aculeatus*) which responded strongly to playbacks of a male displaying (shown in either colour or greytone) clearly and repeatably preferred a coloured display, whereas those that responded less showed no consistent preference for coloured over greytone displays. It will be interesting to test repeatability over longer time periods to see whether variation among females is due to short-term effects, or consistent preferences that are stable over time. Longer-term studies seem preferable if the aim is to estimate genetic heritability. Non-heritable variables which potentially affect female choice should also be controlled for. For example, age is known to influence mate-choice decisions (e.g. insects: Watt, Carter & Donohue, 1986; Ritchie, 1992*a*; fish: Dugatkin & Godin, 1993).

When estimates of repeatability are used to calculate phenotypic variation among females, there is an implicit assumption that female preference functions are being expressed. However, estimates of repeatability, as with those of heritability, vary depending on the environment in which they are calculated. For example, females may express repeatably different preferences in the laboratory, but costly preferences may not be expressed in a more natural setting; leading to all females in the field mating randomly with respect to the tested male trait. Conversely, all females may rank males in the same order in a laboratory experiment. However, the same females may vary in their mate-choice decisions when sampling or assessment costs are increased (as is likely in a natural setting), leading to a positive estimate of repeatability. At present, several research techniques are aimed more at establishing preference functions than total mating preferences. For example, a common neurobiological approach involves the description of auditory tuning curves. Aside from concerns that sensitivity need not indicate preferences (W. Eberhard & W. Wcislo, in preparation), even if tuning curves are reliable predictors of behavioural preferences, differences in choosiness also affect mate choice. The willingness of individuals to translate preference functions into mate choice cannot be directly established using data on peripheral sensory systems (Dawkins & Guilford, 1995). Hence, the absence of variation in tuning curves cannot be equated with the absence of variation in mating preferences. Hopefully, this illustrates our claim that the distinction between 'preference functions' and 'choosiness' is not just semantic. Ideally, we suggest that mate choice be examined under laboratory conditions which will reveal 'idealized' preference functions, and in the field (or less benign laboratory conditions) where variation in choosiness may provide a more realistic estimate of repeatability of mating preferences.

Studies of repeatability are particularly useful when they test for relationships between female traits (some of which may be heritable) and patterns of mate choice.

The concept of 'mating-preference genes' is highly abstract because so little work has been conducted into the proximate mechanisms generating mate-choice decisions. What traits do these genes influence? It is thus difficult to conceptualize mechanisms that maintain population variability in mate choice, especially if some preferences are more costly than others. There is, however, growing evidence that mate choice is related to female body size and body condition (see Section VIII). So familiar, heritable traits such as body size, parasite resistance, growth rate and time of emergence may all play an important role in maintaining heritable variation in mating preferences. There is already a large literature explaining how genetic variation in these traits is maintained (e.g. frequency-dependent selection, temporal and spatial changes in selection). Demonstrating a relationship between heritable traits and mate choice may thus provide an important 'short cut' to explaining variation in mating preferences. To date, most work has been correlational (see Section VIII); experimental manipulations of body size, body condition, parasite load and other traits to determine their effects on mate choice are now needed. Of course, we also need to understand why these traits influence mate choice. The effect they have on reducing the costs of choosiness is an obvious area for research.

Even when heritable variation in mating preferences is absent, genetic effects may still be important. The indirect benefits of choosing particular mates often vary in relation to an individual's genotype, due to differences in genetic compatibility. Inbreeding depression (Thornhill, 1993), optimal outbreeding, kin recognition (Bateson, 1983), risk of hybridization and increasing variability at histocompatibility loci (Potts, Manning & Wakeland, 1991) have all been shown to affect mate choice. The influence of these more 'extreme' genetic effects has yielded a slew of data on mating preferences. Genealogy is often an important aspect of these studies, so the focus is on individuals and their relatedness rather than population averages. For example, research into selective mating based on the major histocompatibility complex (MHC) shows that individual females prefer to mate with partners with different MHC types (reviewed in Zuk, 1994; see also Wedekind *et al.* (1995) for a recent experimental study in humans). These studies also provide vital data on the ontogeny and proximate basis of mating preferences. For example, work on kin recognition shows that the likelihood of mating is partly dependent on the degree of relatedness between potential mates. This is often a consequence of experiences during infancy such as being reared in the same litter, rather than an innate ability to detect kin (Fletcher & Michener, 1987). Similarly, Simmons (1989) has shown that an 'innate' mating bias against kin in the cricket *Gryllus bimaculatus* is strengthened when females experience the pheromones of unrelated males. If the same attention is paid to the history of individuals in studies of mate choice for ornaments, equally interesting findings are likely to emerge (e.g. Barlow, Francis & Baumgartner, 1990).

V. NON-HERITABLE CAUSES OF VARIATION IN MATE-CHOICE DECISIONS

Random mating is often taken as indicative of an absence of mating preferences (Pyron, 1995). However, this is unlikely, as preference functions leading to different ranking of males probably occur in most species due to inevitable biases built into sensory systems (Enquist & Arak, 1993; Arak & Enquist, 1995). Whether these preference functions translate into mate-choice decisions depends crucially on whether

there is also selection for female choosiness (Dawkins & Guilford, 1995). If females mate with the first male encountered, sensory biases are less likely to generate non-random mating, unless these biases affect which males are detected first (but see Arak, 1988). This is a point that has been neglected in some recent discussions of sensory exploitation. Here, we describe some problems with interpreting mate choice in terms of mating preferences. Our review illustrates two main points. First, that some factors lead to mate-choice patterns that mimic heritable variation in mating preferences. Second, that other factors obscure heritable variation in female preferences. We divide these factors into three overlapping classes: environmental, social and female phenotype.

VI. ENVIRONMENTAL FACTORS

(1) *Time and energy costs of sampling*

Costs associated with mate sampling are a potential constraint on optimal mate choice (Gibson & Bachman, 1992). In some cases, females may therefore utilize cost-reducing tactics (Höglund & Alatalo, 1995) which will sometimes reduce the intensity of sexual selection on male traits. For example, female three-spined stickleback (*G. aculeatus*) more readily accept a dull coloured male as a mate when forced to swim against a strong current between successive males (Milinski & Bakker, 1992). Slagsvold *et al.* (1988) found that female pied flycatchers (*F. hypoleuca*) move comparatively short distances when sampling mates, and that the total distance travelled is positively related to ambient temperature. Females move shorter distances when it is colder. They suggest that costs associated with sampling may even cause some females to choose an already mated male (Slagsvold & Dale, 1994). When the distance between nest boxes is increased, females show reduced choosiness as fewer males are sampled. Females are also prepared to suffer direct fitness costs, as reduced sampling leads to more matings with males with nest boxes near the ground. These nestboxes are more likely to suffer predation (Alatalo, Carlson & Lundberg, 1988*a*). In the peacock wrasse (*Symphodus tinca*) whether or not females seek matings with those males that provide parental care is related to search costs (Warner *et al.*, 1995). A theoretical model relating the number of nests sampled prior to mating to the costs of searching and the benefits of parental care closely fitted the predicted changes in female choice behaviour over the breeding season. Female choosiness showed phenotypic plasticity in response to temporal changes in search costs. In general, the spatial distribution of suitable breeding sites has been analysed in terms of the effect on mating systems with regard to the opportunities for males to 'monopolize' females (Davies, 1991). If females are sensitive to sampling costs, however, male density and distribution will also determine other aspects of mating structure by limiting the scope for active female choice.

Very few studies have attempted to calculate directly the energetic costs associated with mate choice in the field. Those that have suggested that they are often not that high. In sage grouse, *Centerocercus urophasianus*, travelling to leks increases daily energy expenditure by only 1% (Gibson & Bachman, 1992). In other cases, energetic costs do appear to influence mate choice (e.g. Milinski & Bakker, 1992). There is greater evidence that time constraints are important (Sullivan, 1990, 1994) because: (i) there is an optimal or limited period in which young can be produced. In temperate birds, for example, reproductive success declines with the date of initiation of breeding (Møller

1994a; see also Backwell & Passmore, in press). (ii) Females are only capable of being fertilized for a short period of time due to physiological constraints. In anurans, for example, females that do not obtain a male will oviposit even in the absence of a male (M. D. Jennions, personal observation). In black grouse, *T. tetrix*, females show a definite desire to mate at certain times (see Höglund & Alatalo, 1995). (iii) Females risk failing to obtain a mate (see Møller, 1992a; Palokangas, Alatalo & Korpimäki, 1992). In pied flycatchers, *F. hypoleuca*, the breeding status of males often changes between successive sampling visits by the same female. Indirect female–female competition for access to mates may also impose time constraints on sampling (see Section VII.3). Although time constraints exist, females generally benefit by spending not only more time sampling more males, but also more time assessing each male (e.g. Getty, 1995). The accuracy of assessment of mate quality probably increases with the amount of time spent monitoring behaviour (Sullivan, 1990, 1994).

(2) Predation risk

Predation risk has pronounced effects on female choosiness (Magnhagen, 1991). Field studies have revealed predation costs associated with mate searching in numerous species [e.g. cicadas (*Cicadetta quadricincta*) (Gwynne, 1987); waterstriders (*Gerris remigis*) (Sih, Krupa & Travers, 1990); and isopods (*Paracerceis sculpta*) (Schuster, 1990); but see Gibson & Bachman (1992)]. Theoretical studies predict that the effort committed to discriminating among mates will decrease as predation risk increases (Hubbell & Johnson, 1987; Crowley *et al.*, 1991). It has been suggested that variation in mating preference among populations in guppies (*P. reticulata*) is partly due to differing risks of predation (Houde, 1993). Females in populations with major fish predators show a reduced preference for males with more orange colouration (Houde & Endler, 1990; Endler & Houde, 1995). One recent study suggests a possible cost to sampling males. Female guppies near brightly coloured males are more likely to be eaten by a predator than are the males (Pocklington & Dill, 1995).

Female crickets (*G. integer*) were offered a choice between long-bout- and short-bout-duration calls in an open phonotaxis arena. They all chose the long-bout call (Hedrick & Dill, 1993). However, if cover in the form of cardboard was provided on the side broadcasting the short-bout calls, some females switched and chose the short-bout call. The proportion of females choosing the short-bout call was positively correlated with the amount of cover provided. Assuming that staying under cover reduces the risk of predation, this study suggests that female choosiness decreases as predation risk increases. Preference functions did not appear to change. Females that chose the short-bout call when it was in the direction of cover were re-tested immediately afterwards in an open arena. Most still chose the long-bout call. In an earlier study, Backwell & Passmore (1990) examined the effect of environmental variation on female phonotaxis in the reed frog *H. marmoratus* by placing perches in one half of a test arena. Two identical calls were broadcast from opposite ends of the arena, and most females approached the call broadcast from the side containing perches. Moreover, although a significant proportion of females usually approach calls of higher intensity (Bishop, Jennions & Passmore, 1995) or lower frequency (Jennions *et al.*, 1994), the tendency for females to use perches was sufficiently strong to eliminate this bias when the 'less preferred' call was broadcast from the side with perches. The situation was further

complicated because the bias for using perches was only evident under reasonably high light levels (full moon) and not under low light conditions (starlight) even though females still use perches in near total darkness. It is not clear why females preferred perches when approaching a call, although reduced predation risk compared to travel on the ground is an obvious explanation. A. S. Rand (personal communication) has also found that light level alters female choice in the tungara frog, *Physalaemus pustulosus*. Light level is implicated in the perceived risk of predation because males reduce calling under low-light intensity conditions when it is more difficult to detect predatory bats (Ryan, 1985).

In a pipefish (*Syngnathus typhle*), mate choice was measured in a two-choice aquarium experiment (Berglund, 1993). In this sex-role reversed species, males choose females. In the absence of a predator, males courted and mated a large female significantly more often than a small female. When a predator was visible, however, males courted both females equally and mated slightly more often with the smaller female. Berglund (1993) interprets this as a consequence of males being 'less choosy'. What exactly does 'choosy' mean? Males were not less choosy in terms of a reduced willingness to sample mates. Both females were continuously visible, and males were actually more active when a predator was present. When both potential mates are 'instantly' available, random-mating suggests that the males no longer have a preference function which ranks a large female above a small female. This may be due to a greater risk of predation when associated with a larger female who is probably a more profitable prey item. Another explanation for the apparent change in preference function is that males were more willing to mate because their estimate of residual reproductive value was lowered. They may have moved between females more often in the hope that at least one of them would deposit eggs. It would be interesting to know whether there is variation among males in the effect of predator presence. Mating was 'random' in the sense that approximately equal numbers of males approached large and small females. However, this could either be because all males ranked large and small females equally, or because a proportion of males now ranked smaller females above larger ones. A very similar effect of predator presence on mate choice was also shown for female choice of males in the sand goby (*Pomatoschistus minutus*) (Forsgren, 1992).

Field studies also suggest that predation risk can influence mate choice. In Uganda kob (*Kobus kob thomasi*), females preferentially mate on leks with good visibility and within leks with males holding territories with better visibility (Deutsch & Weeks, 1992). Under these conditions, mating preferences based on male phenotype may not be expressed because of direct benefits to females mating in areas where predation-risk is lowered.

(3) Territory or resource quality

Mate choice is often based on both male phenotype and the quality of the territory or resources defended by males [topi (*Damaliscus lunatus*), puku (*Kobus vardoni*) (Balmford, Rosser & Albon, 1992); pied flycatcher (*F. hypoleuca*) (Alatalo, Lundberg & Glynn, 1986; Lifjeld & Slagsvold, 1988); two species of fish, *Forsterygion varium* (Thompson, 1986) and *Ophioblennius atlanticus* (Côte & Hunte, 1989) and a fiddler crab, *Uca annulipes* (Backwell & Passmore, in press)]. Predation risk may also vary between territories and may have a greater influence on mate choice decisions than

variation in male phenotype (Deutsch & Weeks, 1992). Whether or not mating preferences for male phenotypes are expressed depends on the distribution of material resources in relation to male phenotype. For example, when material resources are given priority, variability in their distribution is likely to obscure preferences for male phenotype. Lifjeld & Slagsvold (1988) found that the pattern of female mate choice in pied flycatchers (*F. hypoleuca*) was non-random with regard to male plumage when the habitat was homogeneous. In contrast, earlier work in a heterogeneous environment showed that female choice was unrelated to male phenotype (Alatalo *et al.*, 1986).

Changes in female choosiness in relation to different preference functions will also influence mate-choice patterns. For example, females can continue sampling until they mate with a male with a highly ranked phenotype on a highly ranked territory, or they can reduce their mating threshold for one or more of the mate-choice cues. Variation in the costs of choosiness may therefore lead to spatial or temporal variation in the strength of the association between male phenotype and mating success. For example, in the fiddler crab *U. annulipes*, early during each 14 day semi-lunar cycle females mated with larger males whose burrows exceeded a threshold value. Females did not return to previous burrows and the mated male's burrow invariably had a higher 'quality index' than any of the other burrows sampled. Later in the breeding cycle there was no large-male mating advantage, but females still chose to mate in burrows with the highest 'quality index' (Backwell & Passmore, in press). Thus, there appears to have been a change in female choosiness for male size but not for burrow features.

(4) *Environmental effects on signal detection and discrimination*

Earlier we defined preference functions as the order in which phenotypes were ranked. Of course, the shape of the function also influences mate choice. The potential for reversals in the relative ranking of phenotypes increases when functions have flat gradients and there is imperfect assessment of signals (Johnstone, 1994; Wiley, 1994). These errors in assessment may lead to changes in mate-choice decisions. For example, another explanation for the results of Berglund (1993) (see Section VI.2) is that the equal mating success of large and small female pipefish with a predator present was due to males focusing their attention on monitoring the predator rather than assessing the females. Variation in 'attention' affects discriminatory ability in foraging and learning situations and is likely to have equally important effects in mate choice. Getty (1995) provides a recent and interesting review of the optimal period that females should invest in discrimination. His model suggests that when different contexts lead to different levels of selectivity, individuals should assess their own ROC (Receiver Operating Characteristic) curves (which indicate discriminability) in relation to 'their own sensory, perceptual and cognitive constraints'.

Sensory capabilities are influenced by environmental conditions which determine the accuracy of signal detection and discrimination. For example, it is impossible to discriminate between certain colours under certain light conditions (e.g. Milinski & Bakker, 1990). Over evolutionary time, there has been selection on males to use those channels of communication most suited to the environment (Marchetti, 1993). Acoustic signals are particularly sensitive to attenuation and degradation which varies systematically between different habitats. This has led to consistent differences in call structure associated with different habitats (Wiley, 1994). Similarly, when the ability to

discriminate signals varies among habits, females may give preferential weighting to those signals that are most easily discriminated. This may lead to spatial and temporal variation in the characters which influence mate choice.

In several frog species, mating preferences observed in the laboratory are not reflected in the pattern of mating in the field (Gerhardt, 1992). For example, laboratory phonotaxis trials indicate a strong female preference for low-frequency calls in reed frogs (*H. marmoratus*). Although larger males produce lower-frequency calls, a field study of male mating success involving over 1000 males failed to demonstrate a large-male mating advantage (Dyson *et al.*, 1992). In laboratory studies, the ability of female frogs to discriminate calls differing in intensity (Bishop *et al.*, 1995) or frequency (Gerhardt, 1982, 1987) is reduced if the number of speakers broadcasting calls is increased. This suggests that the inability of some frogs to express mating preferences seen in the laboratory may be attributable to the increased acoustic and structural complexity of the natural setting (Telford, Dyson & Passmore, 1989; Gerhardt, 1992). Evidence that female choice can explain non-random mating is sometimes based on mate choice under artificially simple conditions predicting the observed field mating pattern (e.g. a large-male mating advantage). This conclusion may well be correct, but it should be supported by evidence of mate choice in the field. In the case of phonotaxis studies on frogs and insects, it is relatively easy to repeat key laboratory experiments by broadcasting calls in the field and counting the number of females that different stimuli attract. Surprisingly, this rather obvious approach has rarely been used (but see Gibson, 1989).

Gerhardt & Klump (1987) showed that green treefrogs (*H. cinerea*) can only detect calls with an intensity equal to or greater than that of the background chorus (see also Schwartz & Gerhardt, 1989). In a large breeding chorus, this probably limits females to detecting three to five males at any given moment. Unless females actively move around the chorus, mate choice may thus be based on a far smaller set of males than those present at a breeding site. Knowing which males a female is capable of detecting has important implications when determining mating preferences (e.g. Morris, 1989). Forrest & Raspet (1994) provide a detailed model illustrating the difference between passive and active choice and discuss female choice in relation to male spacing in acoustic signallers. They note that the results of phonotaxis studies are difficult to interpret in terms of female sampling tactics without knowledge of female sensory capabilities. In general, better understanding of female neurobiology and sensory capabilities is a prerequisite for any real advance in our understanding of mate choice (see Bennett, Cuthill & Norris, 1994).

How can we distinguish perceptual 'errors' from variation in preferences? Two lines of evidence are available. First, repeatability of female choice should be low if females cannot distinguish stimuli, and mate choice is therefore random with respect to actual mating preferences. Second, if there is a strong bias at the population level for certain signal features, but this preference disappears when the variability in these signals is reduced, then lack of discrimination (rather than lack of preference) is probably responsible (although lack of discrimination is not the only possible explanation for such an effect because reduced variability also lowers the benefits to be gained from choosing). However, even when there is no population-level bias, some females may still be discriminating. Females may vary in their general ability to discriminate

(Jennions *et al.*, 1994), or in their willingness to invest time in discriminating. If discriminating females are rare, there may be no detectable population-level mating bias when sample sizes are small. However, tests of repeatability of choice may still allow researchers to detect the presence of these individuals. In our experience, studies are usually constrained by limited numbers of receptive females rather than by the time available for testing. Repeated testing of individual females may therefore be a worthwhile activity while waiting for additional receptive females.

VII. SOCIAL FACTORS: THE EFFECTS OF CONSPECIFICS

(1) *Interactions between males*

Male–male competition obviously affects female choice if it physically prevents females from mating with preferred males (Trail, 1985). However, more subtle interactions between males can also obscure or alter female mating preferences. One well-studied phenomenon in acoustics is a ‘precedence effect’ whereby females preferentially approach the leading call when two calls are presented in a leader–follower sequence (Greenfield, 1994; Minckley & Greenfield, 1995). This effect may override other preferences. In *H. marmoratus*, when calls are presented in a leader–follower sequence, females prefer the leading call even if it has a higher frequency (Dyson & Passmore, 1988*a*; Jennions, 1994). When calls are presented antiphonally, females preferentially approach the lower-frequency call (Jennions *et al.*, 1994). Leader–follower sequences are generated through male–male interactions, so changes in male behaviour induced by other males affect female mating preferences for low frequencies (Greenfield, 1994). Females also influence males, although the precise adjustments in male call timing vary among species in a manner which appears to depend on the exact nature of the female preference for leading calls (see Minckley & Greenfield, 1995). In general, in acoustically signalling species there is considerable potential for interference between callers. Consequently, there are often very precise interactions between males which act to preserve the structure of their signals (Schwartz, 1994), and thereby influence the subsequent ability of females to discriminate between stimuli (Schwartz, 1987).

Inter-male spacing also influences mate choice in several acoustically signalling species (e.g. *H. marmoratus*: Telford, 1985; *Bufo calamita*: Arak, 1988; *Tettigonia viridissima*: Arak, Eriksson & Radesater, 1990). There may be trade-offs between female preferences for call features and for males that are either clumped or dispersed. Different forms of male–male spacing and chorus organization therefore have strong effects on patterns of mate choice for call features. It is difficult to predict how male spacing will influence mate choice because this depends on both the choice tactics females use as well as on their sensory capabilities (reviewed by Forrest & Raspet, 1994). Female sensory capabilities determine both the number of males that are audible (Gerhardt & Klump, 1987) and the extent to which females can discriminate between neighbours (Telford, 1985).

In the field, male reed frogs (*H. marmoratus*) do not generally interact acoustically with one another once they have started advertisement calling. There is no consistent call alternation or synchronization (Dyson, Henzi & Passmore, 1994). Consequently, leader–follower patterns emerge and switches in leadership between males often occur by chance. Females prefer leading calls as well as low-frequency calls. Given these two

preferences how do they locate males? Continual approaches towards a leading call would be time-consuming if the location of the leader continually changes. In two-choice phonotaxis, females were allowed to begin their approach to a leading call. The leading and following calls were then switched between speakers (Dyson *et al.*, 1994). The likelihood that the female reorientated and continued to approach the leader was distance-dependent. At greater distances, they were less likely to reorientate. In addition, the frequency of the calls also had an effect. When a high-frequency leader was switched to a follower and the low-frequency follower to a leader most females reorientated and approached the low-frequency leader. In contrast, they were less likely to reorientate when a higher-frequency follower was switched to a leader and often continued to approach the now low-frequency follower call. This work summarizes three important points. First, male spacing determines the likelihood that females reorientate towards a new male. Second, male–male interaction patterns determine whether or not the female preference for leader/follower or high/low frequencies is expressed. Third, interactions between preferred traits are often synergistic (see Section IX.2).

Perhaps the most dramatic effects of male spacing patterns on female choice arise with leks (Höglund & Alatalo, 1995). The causes of lekking probably vary from species to species. In ungulates, for example, Clutton-Brock, Deutsch & Nefdt (1993) suggest that the tendency for females to mate on leks is a response to the high risk of harassment from other males when matings are performed in large herds. Other workers have suggested that leks arise because females prefer to mate in places where they can more easily assess several males (Bradbury, 1981). What is evident, however, is that mate choice on leks is often based on phenotypic and environmental features that differ from those used away from leks (Balmford, 1991). One possible reason for this is that sampling on leks is less costly, allowing females to use more discriminatory sampling tactics (Janetos, 1980) such as ‘best-of- N ’ sampling which has been recorded in most lekking species (see Section IX.1). In contrast, this tactic is probably infeasible in, say, a large herd of ungulates and is less likely, or at least the number of males sampled will be far fewer, when males are widely dispersed. On leks, copying the mate choice of others is also more feasible than in other mating systems (Gibson & Höglund, 1992). Most of the species in which mate-copying has been identified are lek breeders (see Section VII.4).

While leks are usually associated with greater scope for female choice, recent ‘blackhole’ models suggest that female ungulates may mate indiscriminately on leks (Clutton-Brock, Price & MacColl, 1992; Stillman, Clutton-Brock & Sutherland, 1993). In these models, lekking and non-random patterns of mating are determined by the relative ability of males to sequester females. Because males on leks are closer together, not only active female choice but also direct male–male competition are more likely. On larger leks, for example, there is a reduction in male mating skew that may be related to increased levels of male aggression (Widemo & Owens, 1995). Whether greater male–male competition hinders or benefits females depends on the extent to which male dominance correlates with female mating preferences. Several studies of lekking species suggest that females do prefer dominant males (Gibson & Bradbury, 1987; Alatalo, Höglund & Lundberg, 1991; reviewed by Höglund & Alatalo, 1995).

(2) *Variability in male phenotypes*

Females can only express mating preferences if there is sufficient phenotypic variation among males to detect differences (Petrie, 1983; Cherry, 1990). Interestingly, sexual traits often show greater phenotypic variation than ordinary morphological traits (Alatalo *et al.*, 1988b; but see Barnard, 1994). Evidence that variation is important comes from field studies where mating is naturally random or weakly skewed with respect to ornament size, but where experimental manipulation of ornaments that increases size variation results in non-random mating (e.g. longtailed widowbirds, *Euplectes progne*, Andersson, 1982; reviewed by Ryan, 1994). Sullivan (1994) suggested that female choice is usually based on the most variable male signals because these traits show the strongest correlation with male mating success (e.g. Ipswich sparrows, *Passerculus sandwichensis*: Reid & Weatherhead, 1990; Great snipe, *Gallinago media*: Fiske, Kålås & Sæther, 1994). E. Forsgren (in preparation) found that female sand gobies, *Pomatoschistus minutus*, are more choosy when variability in male courtship levels is higher. However, it is more difficult to obtain a statistically significant relationship between mating success and male phenotypic traits when variability in the trait is low (N. Wilson, personal communication), and this may also account for the observed pattern. In a model, Real (1990) showed that choosiness increases when there is greater variation in male quality because of the potential increase in benefits associated with mating with a high-quality partner (see also Getty, 1995). If male quality is signalled phenotypically, then greater phenotypic variability is also associated with greater potential benefits of choosiness.

(3) *Female–female competition*

The role of male–male competition and interference in reducing a female's ability to express mating preferences is well known (Thornhill, 1980; but see Trail, 1985). However, with the exception of potentially sex-role reversed species such as doterels (*Charadrius morinellus*) (Owens, Burke & Thompson, 1994), far less attention has been paid to female–female competition. Female–female competition is not only associated with sex role reversal, and may occur in any situation in which there is large variation in male quality (e.g. Petrie, 1989). In lek-breeding peacocks (*Pavo cristatus*), dominant females attempt to monopolize preferred males by repeatedly engaging them in courtship. This results in some subordinate females mating with males with smaller trains (Petrie *et al.*, 1992). In colonial breeding razorbills (*Alca torda*), extra-pair copulation (EPC) occurs on lek-like mating arenas. Females sometimes disrupt EPC attempts by their mates using direct physical aggression towards both their own mate and the extra-pair female (Wagner, 1992). Most mating-system studies focus on the role of females in mate choice, but direct female–female aggression is also important and seems to occur in many species (see Ahnesjö *et al.*, 1993; Rosenqvist & Berglund, 1992). In birds, it may be an important factor in the maintenance of monogamy (reviewed by Slagsvold & Lifjeld, 1994; Eens & Pinxten, in press).

Female competition may sometimes take subtle and indirect forms that do not involve overt aggression. In pair-bonded birds, females may engage in repeated copulation with their mates to reduce the risk of male EPC or of a second female settling on their territory (Petrie, 1992; Petrie & Hunter, 1993; Hunter *et al.*, 1993). When

mating is positively assortative with respect to quality, and higher-quality females are better at preventing EPC, this may make it more difficult for low-quality females to mate with high-quality males. There is evidence both for assortative mating on the basis of 'quality' and that females preferentially seek EPC with higher-quality males (e.g. Houtman, 1992; Kempenaers *et al.*, 1992).

There have, however, been few attempts to test whether females vary in their ability to prevent EPC or the formation of additional pair-bonds by their partner. What traits or tactics might be responsible for such variation (Petrie & Hunter, 1993; Slagsvold & Lifjeld, 1994; Kempenaers, 1995)? Whittingham, Dunn & Robertson (1994) investigated the 'multiple copulation as mate guarding' hypothesis in tree swallows (*Tachycineta bicolor*) and concluded that it did not explain why females mate multiply (but see Eens, Pinxten & Kempenaers, 1995; Whittingham, Dunn & Robertson, 1995). In contrast, there is good evidence from both observational (Eens & Pinxten, 1995) and experimental studies (Eens & Pinxten, in press) that female European starlings (*Sturnus vulgaris*) do mate guard by soliciting copulations. When a second female was introduced to a caged pair, the original female increased her rate of copulation solicitation. It remains to be seen, however, whether females vary in the success with which they employ this and other tactics.

In some poison-dart dendrobatid frogs (e.g. *Dendrobates auratus*), female-female competition is not associated with classic sex-role reversal. Rather, it seems to involve a defending female preventing other females from mating with a male with whom she has previously mated (Summers, 1989, 1992). This may occur because *per capita* tadpole survival is lowered when males tend more than one brood (Summers, 1990). Repeated female courtship of males in dendrobatid frogs has also been interpreted as an attempt to prevent males from mating with additional females (Summers, 1989). Female brentid weevils (*Brentus anchorago*) also disrupt courtship and copulation attempts. This 'spiteful' behaviour is thought to reduce the number of females ovipositing and increase larval survival rates (Johnson, 1982). In flycatchers (*F. hypoleuca*), resident females prevent or delay other females from settling which increases the amount of paternal care their own offspring receive (Slagsvold & Dale, 1994; Dale & Slagsvold, 1995). Female-female aggression may also limit the ability of females to search for mates (Dale, Rinden & Slagsvold, 1992). Similar female-female aggression has also been reported for blue tits, *Parus caeruleus* (Kempenaers, 1994, 1995). The general effect of these female-female interactions in dart-frogs, weevils and birds is potentially to constrain the expression of mating preferences of at least some females (see also Møller, 1992a). The outcome of these constraints in generating variation in female fitness is not well studied. However, when choice is for direct benefits, the costs of a sub-optimal choice are likely to be considerable. Even in species in which there are no obvious material benefits associated with mate choice (but see Fox, McLennan & Mousseau, 1995), choice may have benefits in terms of increased offspring viability (Norris, 1993; Petrie, 1994). The inability to choose freely may therefore generate substantial variation in offspring fitness.

(4) *Female mate copying*

Recent studies indicate that individual mate-choice decisions are not always independent and that females may copy one another (reviewed by Pruett-Jones, 1992;

Gibson & Höglund, 1992; Höglund & Alatalo, 1995). Earlier theoretical work on lekking species suggested mate-choice copying because unanimity of choice appeared to be greater than expected on the basis of independent female choice (Bradbury, Verhencamp & Gibson, 1985). Mate copying has been implicated in skewed mating patterns in two species of manakin (*Pipra erythrocephalus*, *Manacus manacus*) (Lill, 1974, 1976), black grouse (*Tetrao tetrix*) (Höglund *et al.*, 1995), sage grouse (*Centrocercus urophasianus*) (Gibson, Bradbury & Verhencamp, 1991), Lawes parotia (*Parotia lawesii*) (Pruett-Jones & Pruett-Jones, 1990), fallow deer (*Dama dama*) (Clutton-Brock *et al.*, 1988; Clutton-Brock, Hiraiwa-Hasegawa & Robertson, 1989; but see McComb & Clutton-Brock, 1994), guppies (*P. reticulata*) (Dugatkin, 1992) and mollies (Schlupp, Marler & Ryan, 1994). There is also evidence from two species of antelope (*Kobus kob*, *K. leche kafuensis*) that females preferentially mate on lek territories where other females have previously been. Experimental relocation of soil suggested that females use substances contained in urine to assess earlier female presence, and preferentially mated on territories with higher female visitation rates (Deutsch & Nefdt, 1992). Most cases in which mate copying is thought to occur involve lekking species.

Mate-choice copying has been explained in at least two ways. First, as a tactic that reduces the costs of sampling. Although sampling on leks does not appear to be costly in terms of energetics (e.g. Gibson & Bachman, 1992) or predation risk (see Höglund & Alatalo, 1995), time constraints may be important (see Section VI. 1). Losey *et al.* (1986) developed a simulation model in which both the costs and benefits of copying differed from those of direct mate assessment. They showed that due to frequency-dependent selection (not everyone can copy), copying and direct assessment may yield the same overall fitness payoffs. If copying does reduce costs, we might expect females to be more likely to copy when they are vulnerable to sampling costs. Thus, females in poor condition, with high parasite loads or that are inexperienced should be more likely to copy (Pruett-Jones, 1992). Dugatkin & Godin (1993) found that young guppies (*P. reticulata*) were more likely to copy the mate-choice decisions of older guppies. In sage grouse (*C. urophasianus*) and black grouse (*T. tetrix*), younger females mate later than older females and are thus more likely to be the copiers (Höglund & Alatalo, 1995). Age-related changes in propensity to copy may have important implications. Kirkpatrick & Dugatkin (1994) modelled the copying of older females by younger ones where preferences were 'culturally' acquired. The outcome was the coevolution of preference and trait and a decreased likelihood that female preferences will maintain novel male traits. In general, if female preferences become more directional with age or experience due to increased investment in sampling (i.e. greater choosiness) or through developmental changes in preference functions then copying may strengthen the intensity of directional sexual selection on preferred male traits. Experimentally, there seems to be room for future work manipulating the costs of mate choice to investigate whether copying can be increased. Parasite load, body condition and perceived parasite risk could all be altered in laboratory experiments with, for example, guppies to determine the effect on copying behaviour.

Second, copying may be a mechanism whereby females can quickly obtain more precise information about potential mates. If the mate-choice decisions of others contain information about specific males, then watching the mate choice of others

decreases the likelihood of choosing an inappropriate mate (Bikchandani, Hirschleifer & Welch, 1992). However, this may also lead to so-called 'information cascades' (Gibson & Bachman, 1992) in which an increase in reproductive skew may arise due to amplification of initially small variations in female visitation rates that are unrelated to preferred male traits (Deutsch & Nefdt, 1992). Whether copying leads to stronger directional selection or arbitrary trends depends crucially on whether the mate choice of copied females is random or not. It is less likely to be random when some females copy and others actively choose. 'Information cascades' are more likely when all females show a propensity to copy (Bikchandani *et al.*, 1992). Again, we need data on variability among females. How much variability is there among females in their propensity to copy?

A distinction is often drawn between active copying of mating decisions of other females and a general preference for association with other females in aggregations ('conspecific cueing') (McComb & Clutton-Brock, 1994). However, this distinction is reminiscent of that between active and passive mate choice which was strongly criticized on the grounds that it confused proximate and ultimate questions (see Sullivan, 1989). Both aggregation and copying have the same ultimate effect whereby variation in male mating success is increased due to females approaching sites where other females either have been or are present. The proximate mechanisms responsible may, of course, differ among species and knowing what they are is therefore necessary for a full understanding of why females influence each others' mating decisions.

(5) *Density and the operational sex ratio*

The operational sex ratio (OSR) and the spatial distribution of the two sexes have long been key elements in theoretical discussions of sexual selection and the evolution of mating systems (reviewed by Davies, 1991; Clutton-Brock & Parker, 1993). Even so, much remains to be discovered about the proximate mechanisms leading to behavioural changes, and the validity of some predictions of OSR theory are now also questionable (see Arnold & Duvall, 1994). For example, inter-sexual competition can occur in both the choosy and the non-choosy sex (e.g. Petrie *et al.*, 1992). When females are the more aggressive sex, this need not mean that female mate choice does not occur, or that male mate choice will occur (Summers, 1992; Owens *et al.*, 1994). The extent of variation among individuals is an element that should be incorporated into theoretical models more often. It determines the benefits of mate choice and may also affect the costs of choosiness. In the same way that the OSR and density influence alternative mating tactics of males (Lucas & Howard, 1995), they may also influence alternative sampling tactics and mate-choice decisions of females.

If the OSR can be used to predict changes in mating behaviour then animals are either able to estimate the OSR or, more plausibly, there are proximate cues related to the OSR. How are cues associated with the OSR and density likely to affect mate choice? One possibility is that they affect the costs of sampling. (1) When the density of the chosen sex is lower, there are increased distance, energetic and time costs to sampling (Real, 1990). These should lead to a reduction in choosiness. (2) There is an increased risk of failure to mate or, in pair-bonded species, of not receiving assistance with parental care, when the OSR is less biased towards the chosen sex (Møller, 1992*a*). Females may therefore adjust preferences or choosiness in response to the rate at which

they encounter other females. In pied flycatchers, *F. hypoleuca*, sampling females may use the rate at which they encounter other sampling females (Dale & Slagsvold, 1995). Females may also become less choosy or change their preferences as they encounter a greater proportion of males that are already paired. In some species, the OSR may be such that 'sex-role reversal' occurs and the gender of the choosy sex changes (Gwynne, 1991). Role reversal, however, is only a highlight in a continuum of changes in choosiness. Even before role reversal, there may be changes in the extent to which less attractive individuals can express their mating preferences due to increased likelihood of rejection. The perceived OSR may therefore have effects on sampling and mate choice that differ depending on a female's phenotype. Less attractive females may become less choosy at lower female-biased OSR values than more attractive females because the costs of choosiness are negatively correlated with attractiveness (see Section VIII).

An increase in choosiness at higher densities of the chosen sex has been shown in pied flycatchers (*F. hypoleuca*) (Alatolo *et al.*, 1988a), a katydid (*Kawanaphila nartee*) (Shelly & Bailey, 1992) and kestrels (*Falco tinnunculus*) (Palokangas *et al.*, 1992). Milinski & Bakker (1992) have also noted that their experimental manipulation of the costs of sampling in stickleback (*G. aculeatus*) mimicked variation in male density. However, higher male density is not always associated with increased female choosiness. At high male densities or strongly male-biased OSR values, females may be so persistently courted by males that it is less costly to accept matings than to try to evade males (e.g. waterstriders, *Gerris* spp.: Rowe *et al.*, 1994), leading to a reduction in the intensity of sexual selection on male phenotypic traits. Allen & Bailey (1994) also found that the propensity of male crickets (*Requena verticalis*) to mate did not increase when the encounter rate with females was experimentally lowered (cf. results of Shelly & Bailey, 1992).

Several experimental studies on a range of taxa show that the OSR influences choosiness. In a two-choice test, male pipefish (*S. typhle*) preferentially mated with a large female when the OSR was female-biased, but were equally likely to mate with large or small females when the OSR was male-biased (Berglund, 1994). In milkweed beetles (*Tetraopes tetraophthalmus*), males were more choosy when the OSR was female-biased, although they continue to engage in contests with other males (Lawrence, 1986). In field crickets (*Gryllus pennsylvanicus*), females were more choosy when the OSR was male-biased (Souroukis & Murray, 1995). (For additional examples see Gwynne, 1991 and Vincent *et al.*, 1992.) More recent studies have also attempted to explain variation in the OSR in terms of environmental features such as food availability (Gwynne & Simmons, 1990), ambient temperature (Ahnesjö, 1995) and parasite levels (Simmons, 1994). Knowledge of these features may also be used to predict variation in mate-choice patterns (see Gwynne & Brown, 1994, for an example of inter-specific variation in response to the same treatment).

VIII. FEMALE PHENOTYPES

Several studies show a relationship between female phenotype and that of their mates. This may occur because the direct costs and benefits of mating with certain males differ among females. For example, larger females may require larger males to ensure that all their eggs are successfully fertilized, or smaller females may be unable

to withstand the cost of mating with a large male (Ryan, 1985; Robertson, 1990; Bourne, 1993). Mechanical constraints on pairing may also lead to positive assortative mating in some species (review: Brown, 1993). There is also evidence that short-term female condition influences mating behaviour. In water mites, *Neumania papillator*, female hunger level determines their responsiveness to males. Males exploit the female's attractiveness to stimuli associated with food by mimicking cues produced by prey items (Proctor, 1991). Hungry females are more likely to mate with a range of male phenotypes. In bullies (*G. breviceps*), parasitized females make fewer visits to potential mates and are more likely to mate with small males than are unparasitized females (Poulin, 1994). In a bush cricket (*R. verticalis*), parasitized females attempt to mate more frequently, presumably because they wish to obtain nutrients from male spermatophores (Simmons, 1994). This leads to increased choosiness by males, which should, in turn, have a negative effect on the ability of less attractive females to mate with preferred males.

A female's phenotype may predict mate-choice behaviour because it affects sampling costs. In pied flycatchers (*F. hypoleuca*), there is a positive correlation between an index of body condition and the distance females travel prior to choosing a mate (Slagsvold *et al.*, 1988). In redlipped blennies (*O. atlanticus*), larger females travelled further to reach mates, had more scars (which are sustained during sampling by attacks from damselfish) and mated with larger males. This suggests that they were prepared to pay higher costs to mate with larger males who provide better parental care (Reynolds & Côte, 1995). Choudhury & Black (1993) found that larger, heavier barnacle geese (*Branta leucopsis*) females formed more 'trial liaisons' prior to pairing; and Rintamäki *et al.* (1995) found that large female black grouse (*T. tetrix*) with a high body mass visited more males prior to mating. In some species, males seek out females for mating purposes. In the common shrew (*Sorex araneus*) there are two types of males. Type B males who are larger at the start of the breeding season are more likely to move and encounter females, while Type A are more stationary (Stockley, 1994a). In contrast, Fiske & Kålås (1995) found a trend for larger female great snipe (*Gallinago media*) to spend less time on the lek prior to mating than did smaller females. In general, however, it appears that females with greater energy reserves or larger body size increase the time period or area over which they sample, leading to variation in mate choice which may be unrelated to preference functions. There is a need for further experimental manipulation of female condition, body size, perceived estimates of residual reproductive value and other traits which should affect sampling behaviour and mate choice. It is important to note, however, that these effects are unlikely to be apparent in low-cost, two-choice experimental set-ups in which mates are simultaneously and instantly available. Researchers should therefore attempt to design experiments in which sampling costs are more similar to those in the field (e.g. Milinski & Bakker, 1992).

In species with mutual mate choice, females vary in their attractiveness to males (Brown, 1990; Jones & Hunter, 1993). This should lead to positive assortative mating with respect to attractiveness (Burley, 1983). As preferred males drop out of the pool of potential mates, some females may be forced to mate with less-preferred males (Brown, 1990). Less-attractive females may partly solve this problem by seeking EPC with more attractive males (Møller, 1988, 1992a); Houtman, 1992; Kempnaers *et al.*,

1992). In contrast, attractive females may become more choosy in their initial choice of mate, because they stand a smaller risk of not obtaining a high-quality male, or of failing to mate (Petrie & Hunter, 1993). If this is true, females must first assess their own attractiveness relative to that of other females. We are unaware of data collected to test whether this occurs.

Alternatively, the preference functions of females may differ. If unattractive females 'know' they are unlikely to retain a high-quality mate, they may prefer lower-quality males over higher-quality males. Mating with a high-quality male carries several potential costs: a greater risk of desertion; of a secondary female attempting to pair with your mate and thereby reducing male care for your own offspring; of disease transfer from a mate who performs more EPC (Birkhead & Møller, 1992); of reduced parental care by attractive males (Burley, 1988; de Lope & Møller, 1993; Møller, 1994*c*). Variation in a female's ability to compensate for these costs may lead some females to choose low-quality males. This may explain repeatable female choice based on tail length in barn swallows (*H. rustica*) (Møller, 1994*b*). Tail length appears to be an honest signal of male quality in this species (Møller & de Lope, 1995). In the absence of differing costs, it is perplexing why all females do not prefer long-tailed males.

IX. HOW DO FEMALES CHOOSE MALES?

(1) *Sampling tactics*

Until recently, the average sexual selection field study consisted of monitoring males and counting the number of females they attracted. But how do females find these males? How do they succeed in mating with males that are larger than average, or have longer tails or louder calls? For these and related questions, there have been few empirical answers, but several theoretical investigations have been carried out. A major issue motivating this modelling has been the effect of preference costs on the outcome of different models for the sexual selection of male ornaments (Pomiankowski, 1988; Reynolds & Gross, 1990; Iwasa *et al.*, 1991; Kirkpatrick & Ryan, 1991; Andersson, 1994). In many models, the direct cost of choice is assumed to be outweighed by indirect benefits (e.g. Iwasa *et al.*, 1991). Whether this is generally the case remains to be shown. In rhesus macaques (*Macaca mulatta*), females that spent time in proximity to lower-ranking males (which is a correlate of copulation rate) suffered increased rates of attack by dominant males (Manson, 1994). This suggests that females *are* prepared to incur direct costs from mating with lower-ranking males. However, as in most cases it is unclear whether the benefits are indirect, direct or both. In general, the applicability of many models of female-preference evolution are sensitive to the costs and extent of direct selection on choosiness (e.g. see Pomiankowski, 1988; Kirkpatrick & Barton, 1995). Empirical data may therefore have a major impact on the plausibility of some mathematical models.

Theoretical studies have also related adjustment of searching behaviour and choice tactics to variation in predation risk (Hubbell & Johnson, 1987), mate density (Crowley *et al.*, 1991), costs of memory allocation (Hutchinson, McNamara & Cuthill, 1993; Roitberg, Reid & Li, 1994) and time constraints (Real, 1990). Theoreticians have proposed at least six tactics that can be used when choosing mates (Parker, 1978, 1979, 1983; Janetos, 1980; Wittenberger, 1983; Real, 1990; Dombrovsky & Perrin, 1994). Examples of species in which these different tactics are thought to occur are presented

in Table 1. (1) Random mating tactic: accept the first mate encountered. (2) Fixed threshold tactic: sample sequentially and accept the first mate that exceeds a set criterion. Mating always occurs with the last male sampled. (3) Sequential comparison tactic (Wittenberger, 1983): sequentially compare mates until the most recently encountered is of lower quality than the previous encountered, then accept the previously encountered male. This always leads to mating with the penultimate male in a sampling sequence. (4) One-step decision tactic (Janetos, 1980) or sequential search rule tactic (Real, 1990): sample until the value of the mate encountered is greater than that expected from continued searching. The sequential search rule is a refinement of the one-step decision tactic in that it also considers the costs associated with continued searching. As with the fixed threshold model, females generally mate with the last male sampled. The difference is that this male may not have the highest value for the preferred criteria. The model can be considered as a modification of the threshold model, in which the threshold varies through time in relation to the costs of sampling and the expectation of finding a male that will exceed the present threshold. If females can recall the positions of previous males, and their threshold is subsequently lowered, they may sometimes return to previously sampled males (Fiske & Kålås, 1995). (5) Pooled comparison ('Best-of- N ') (Janetos, 1980): sample N males and then accept the male with the highest value for the preferred trait(s). This is potentially the most rewarding, but also the most costly tactic (Real, 1990). (6) Optimal stopping rule (Dombrovsky & Perrin, 1994): this rule is similar to tactic 4, but differs technically in that it makes the more realistic assumption that the choosy sex does not know *a priori* the distribution of quality in the chosen sex. The model does, however, assume that a female knows *a priori* the total number of samples she can make (this assumption is shared with tactic 4). This model makes several predictions concerning the length of the sampling period, the existence of a 'previous-male effect' and that this latter phenomenon will not only be confined to the previous male sampled, but to males earlier in the sequence as well. The rule is designed to maximize a female's chances of mating with the best male encountered but it ignores any costs of choice and treats the second-best male as no better than the worst and is therefore unlikely to be relevant to biological male choice.

In practice, it has proved difficult to distinguish which tactics are being used by females in the field. This may be partly due to variation among females. Tactics need not be invariant within a species. They vary in their costliness, and not all females may be able to use the most expensive tactics. Resolving this problem may require data on successive sampling-mating sequences by individual females, with suitable statistical controls for age and size-effects. For example, Fiske & Kålås (1995) have shown that experienced great snipe (*G. media*) females are more likely to return to mate with a previously sampled male than are inexperienced females. In spite of these difficulties, several trends have emerged from field and laboratory studies of sampling behaviour.

(1) Mate choice in many species that sample sequentially involves adaptive searching. That is, females adjust their threshold for acceptance in relation to the phenotype of previously sampled males. Choice is relative, not absolute. A 'previous-male effect' has been reported in zebra finches (*Taeniopygia guttata*) (Collins, 1995), stickleback (*G. aculeatus*) (Bakker & Milinski, 1991) and mottled sculpin (*Cottus bairdi*) (Brown, 1981; Downhower & Lank, 1994). M. L. Reid & B. D. Roitberg (cited in Roitberg *et al.*,

Table 1. Presumed mate-choice tactics based on field studies in which female sampling behaviour was monitored

(The following are lekking species: *Gallinago media*, *Pavo cristatus*, *Rupicola rupicola*, *Tetrao tetrix* and *Parotia laevesii*.)

Species	N (females)	Sampling tactics	No. of males sampled mean (range)	Percentage copulating with first male	Source
Fiddler crab (<i>Uca annulipes</i>)	50	Fixed threshold for burrow features, but preferentially visited the burrows of larger males	Up to 24	—	Backwell & Passmore (in press)
Great snipe (<i>Gallinago media</i>)	33	Pooled comparison or possibly sequential search rule	2.9 (1-10)	36	Fiske & Kálás (1995)
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	11	Pooled comparison or sequential search rule	5.9 (3-11)	0	Bensch & Hasslequist (1992)
Barnacle geese (<i>Branta leucopsis</i>)	39	40% one-step decision rule 60% sequential comparison	1.6 (1-6)	51	Choudhury & Black (1993)
Laves' parotia (<i>Parotia laevesii</i>)	—	Pooled comparison	Up to 17	0?	Pruett-Jones & Pruett-Jones (1990)
Pied flycatcher (<i>Ficedula hypoleuca</i>)	20	Pooled comparison but with repeated visits to males/sequential comparison	4.5 (1-10)	20	Dale <i>et al.</i> (1992)
Peacock (<i>Pavo cristatus</i>)	12	Pooled comparison / threshold/sequential comparison	3.5 (3-7)	0	Hovi & Rätti (1995)
Cock-of-the-rock (<i>Rupicola rupicola</i>)	11	Threshold or sequential comparison or pooled comparison	3 (2-5)	0	Petrie, Halliday & Sanders (1991)
Black grouse (<i>Tetrao tetrix</i>)	38	Pooled comparison	3.9-4.9 ¹	0?	Trail & Adams (1989)
Goby (<i>Pomatoschistus minutus</i>)	31	Pooled comparison	4.9 (2-9)	0	Rintamäki <i>et al.</i> (1995)
	26	Threshold criteria or one-step decision rule	2.5 (1-13)	54	E. Forsgren (in preparation)

¹ Range of means between years (N = 4 years).

1994) have shown that female bark beetles *Ips pini* show a greater willingness to mate with intermediate-sized males when they have first been exposed to small males than when first exposed to large males. In the katydid *Scudderia curvicauda*, females showed increased responsiveness over several playback trials, suggestive of a reduction in their mating threshold (Tuckerman, Gwynne & Morris, 1993). In balloon flies (*Empis borealis*), males visit swarming females. They do not appear to be able to assess absolute female size, but can detect relative size within a swarm, preferring larger females (Svensson & Peterson, 1994). Relative choice also occurs in *Drosophila littoralis* and *D. montana* (Hoikkala & Aspi, 1993). Work on sex-role reversal in katydids and crickets suggests that there is considerable plasticity in mating-decision rules in insects (Gwynne, 1991). (For excellent reviews of learning in insects and potential constraints on optimal mate choice see Papaj & Lewis, 1994.) Other studies showing that choosiness changes in relation to OSR, encounter rate or other factors that increase the costs of sampling also support the claim that mating preferences are phenotypically plastic (see Sections VI. 1–2, Section VII. 5).

In some species, there is evidence for fixed mating preferences. Females may have innate preferences for certain male phenotypes. For example, in two-choice tests, naive virgin female guppies showed a stronger response to a male with a greater amount of orange colouration (Brookes & Caithness, 1995a). In cockroaches (*N. cinerea*) there appear to be fixed mating thresholds for male pheromones (Moore & Moore, 1988). A fixed-threshold preference for male comb size has also been reported for red junglefowl (*G. gallus*) (Zuk *et al.*, 1990). In the fiddler crab *Uca annulipes*, there also appears to be a fixed threshold for burrow features (Backwell & Passmore, in press). In general, however, it is hard to see how fixed preferences can persist. In poor years, many males probably fall below a fixed threshold and if females really are inflexible they should refuse to mate. In almost all species there is probably a time-dependent reduction in mating threshold.

(2) There is considerable variability among females in the number of males sampled. In many field studies, females often mate with the first male encountered. For example, E. Forsgren (in preparation) found that 54% of female sand blennies (*P. minutus*) mated with the first male encountered, while others sampled up to 13 males. In barnacle geese (*Branta leucopsis*), 51% of females settled with the first mate encountered, while others sampled up to six males (Choudhury & Black, 1993). In great snipe (*G. media*), 58% of females mated on the first observed visit to a male's territory, others visited up to 13 males (Fiske & Kålås, 1995) (see Table 1). It is not yet clear whether this variation reflects differences in female receptivity, choosiness, mating-preference thresholds, sampling tactics or is simply the result of stochastic variation (i.e. some females encountered preferred males early in a mating sequence).

(3) Real (1990) suggested that the sequential search rule is more likely to be used than the pooled comparison when sampling costs exist (*contra* Janetos, 1980). However, in several species where females use the pooled comparison tactic, there appear to be substantial search costs. For example, the pooled comparison tactic has been reported for some females in pied flycatchers (*F. hypoleuca*) (Dale *et al.*, 1990, 1992; Hovi & Rätti, 1995), great reed warblers (*Acrocephalus arundinaceus*) (Bensch & Hasslequist, 1992) and a damselfish (*Chrysiptera cyanea*) (Gronell, 1989). The pooled comparison tactic does seem more common in species that lek, however, and has been reported in

most well-studied species (see Table 1). This is consistent with the claim that the costs of sampling are lower on leks, allowing a more costly sampling tactic.

(2) *How many cues do females use?*

Many early studies analysed female choice based on the implicit assumption that females only assessed males using a single cue. In fact, the use of multiple cues is probably universal (e.g. Burley, 1981; Zuk, Ligon & Thornhill, 1992; Kodric-Brown, 1993; Choudhury & Black, 1994; Borgia, 1995). Most empirical work shows that behavioural traits, such as rate or intensity of display, influence female choice (reviewed by Ryan & Keddy-Hector, 1992). So even when there is only one obvious morphological ornament, choice is probably based both on display features and ornamentation (cf. Møller & Pomiankowski, 1993*b*). Recently, theoreticians have begun to model the evolution of multiple female preferences (Pomiankowski & Iwasa, 1993; Iwasa & Pomiankowski, 1994; R. A. Johnstone, in preparation). Unfortunately, little is known of the rules females use to weight the value of different signals. This is a frustrating gap in our knowledge which can often lead to erroneous conclusions. For example, some traits show no relationship with male mating success and are dismissed as irrelevant to female choice. However, they may still be important to the extent that they must exceed a threshold value (which all sexually active males fulfil) before females will consider males as potential mates (analogous to the ante in betting; Kodric-Brown & Brown, 1984; Ligon & Zwartjes, 1995*b*) (see Brookes, in press). Females may also discard or add criteria depending on environmental conditions. For example, Thornhill (1987) found that female scorpionflies (*Panorpa latipennis*) accepted males with prey items as mates in a situation in which males could not always procure high-quality items.

There is some evidence that females only pay detailed attention to condition-dependent cues that signal male quality, and that in each species only a single cue is used (Møller & Pomiankowski, 1993*b*; Iwasa & Pomiankowski, 1994). This conclusion is based on data relating to patterns of fluctuating asymmetry, the use of which as an index of condition-dependence has been questioned (Balmford, Jones & Thomas, 1993*b*; Brookes & Caithness, 1995*b*; Jennions, in press). This finding also conflicts with the observation that in well-studied species different investigations often find that different traits are correlated with male 'attractiveness' or mating success. For example, in guppies (*P. reticulata*), tail length, display rate, parasite load, different patterns of colouration and body size have all been implicated (Endler, 1995). Similarly, long-term studies tend to show considerable between-year variation in the extent to which different traits are correlated with mating success (Fiske *et al.*, 1994).

The manner in which females utilize information from multiple cues is not clear. There are several possibilities:

(1) They may treat them in a hierarchical fashion and only use lower-order cues to discriminate between males when higher-order ones show low variation or are difficult to discriminate (Zuk *et al.*, 1992; Ligon & Zwartjes, 1995*b*).

(2) Females may assess several cues simultaneously and give different weightings to each. If an overall 'index' of attractiveness is constructed in this fashion, it raises the intriguing possibility that males can be equally attractive in different ways. This may provide a partial explanation for the presence of continued heritable variation in sexually selected traits, especially if the weighting given to certain traits increases when

they become less abundant resulting in frequency-dependent selection. If traits that are more variable among males are given a higher weighting, stronger selection on these traits may reduce variability and then lead to other traits gaining higher weighting. With an overall 'index', identical female preferences can lead to females choosing males with different values of a single cue.

(3) It is also possible that traits which researchers characterize as different are not perceived as such by animals (R. C. Brookes, personal communication). For example, researchers may speak of amount of black, orange and blue colouration as three separate traits. It is possible, however, that these traits all contribute to net colouration, which is what the female assesses. In the fiddler crab *U. annulipes*, burrows in which females mated differed significantly from those that were sampled in six out of ten measured variables. It is unlikely, however, that each variable was independently assessed, given that females spend only a short amount of time in sampled burrows (e.g. Christy & Schober, 1994). It is more probable that each variable contributed towards the general suitability of the burrow (Backwell & Passmore, in press).

(4) Some sexual traits may not be direct choice cues but rather act as amplifiers of variation in other cues (Hasson, 1991). However, in a series of interesting experiments Brookes (in press) has shown that a trait may act as both an amplifier of another trait and also itself be selected for. Brookes & Caithness (1995*b, c*) found that only orange colouration was correlated with male mating success in a population of feral guppies (*P. reticulata*). Although there was no correlation between black colouration and male mating success, a preference for males with black spots was revealed when black spots were removed by freeze-branding. Even more intriguing was that when black spots were removed, the amount of orange colouration no longer correlated with attractiveness to females (Brookes, in press). This suggests that melanin acts both as a mate-choice cue and as an 'amplifier' of difference in orange colouration (Hasson, 1991). This work also illustrates the difficulties in identifying whether or not a trait is used in mate choice when some traits (e.g. orange colouration) are more important than others (e.g. black colouration).

To understand how females use multiple cues, we probably need to know what information each cue provides. Several hypotheses based on information-content have been proposed for the evolution of multiple male traits (reviewed by Møller & Pomiankowski, 1993*b*): (1) multiple messages, whereby each trait conveys a different type of information about the male (e.g. parasite resistance, recent food intake, carotenoid intake); (2) redundant signals: each signal on its own may not provide sufficient information for accurate assessment, either because males can 'cheat' when only one signal is involved, or because female discrimination improves when they can combine estimates of quality from several different traits; (3) unreliable signals: this suggests that most traits do not provide information about male quality (i.e. are non-condition-dependent Fisherian traits) and are maintained by weak female preferences which are not particularly costly (Pomiankowski & Iwasa, 1993; Iwasa & Pomiankowski, 1994). In support of this, Møller & Pomiankowski (1993*b*) note that multiple ornamental traits are most often found in lekking species in which sampling costs are probably low; (4) in addition to these information-based explanations, another possibility is that different cues function at different distances. For example, in the spotted bowerbird (*Chlamydera maculata*), bones spread around the bower may act to

attract females (they are bleached white and visible from a distance). Glass nearer the bower is encountered later and may act to stimulate the female to mate (Borgia, 1995).

Only when the full set of choice cues and the relative importance attached to each is known, can we address the real extent of variation in female preferences. Being realistic, this is probably an unattainable goal; however, studies in which two or more cues are varied simultaneously should be conducted (see Zuk *et al.*, 1992). Historically, the emphasis has been on manipulation of a single cue while others are held constant (reviewed in Gerhardt, 1992). This work has shown us which traits are potential cues in mate choice. However, only by offering females the choice between different combinations of traits can we test the relative importance of each cue. There is also a strong likelihood that cues may interact in a synergistic manner. For example, female black grouse (*T. tetrix*) prefer to mate with males without damaged tails and also preferentially mate on the central territories on the lek. The effect of tail damage on mating success varies in relation to the position of the male on the lek (Höglund *et al.*, 1994). Similarly, Møller (1992*b*) found that tail asymmetry is more strongly discriminated against in short-tailed males than long-tailed males in barn swallows (*H. rustica*). A final potential problem is that the number of cues females use may vary. For example, females may use fewer cues when sampling costs are increased. This explanation has been proposed to account for differences between species in the number of ornaments (Møller & Pomiankowski, 1993*b*), but it may also account for within-species differences when sampling behaviour shows phenotypic plasticity.

X. CONCLUSIONS

In general, sexual-selection studies have paid less attention to individual variation among females than that among males (Rosenqvist & Berglund, 1992; Ahnesjö *et al.*, 1993). There are practical reasons for this. In many species, males are sexually active and court for long periods, whereas females are only sexually receptive for a short time. Males are often gaudy and conspicuous, while females are cryptic and harder to locate. Males vary widely in their mating success, while it is less obvious how female fitness varies in relation to mating decisions. In spite of these difficulties, we hope this review will convince researchers that studies focusing on females as individuals rather than 'the female response' are worthy of greater attention. Studies of female sampling behaviour may help us to understand: variation in the size and number of male ornaments (see Sections II and IX. 2); the maintenance of heritable variation in female preferences (see Sections IV. 2 and VIII); the size of the benefits provided by choosiness (see Section II); the evolutionary history of preferences and preferred traits (see Section IV. 1); and the general design of male traits (see Section VI. 4).

There is clearly still much to learn about how females choose males, and why different females make different choices. We suggest that one profitable approach will be to determine whether variation among females in the costs of choosiness really does influence mate choice. It should be comparatively easy to manipulate costs (e.g. handicapping females, manipulating parasite loads) and determine the subsequent effects on mate choice. If true, then studies into the heritability of traits associated with the ability to withstand costs may provide the quickest route to increased understanding of the maintenance of heritable variation in female mating preferences. This work may also provide information on the magnitude of the benefits associated with mate choice.

Phenotypic plasticity in choosiness in relation to small changes in the costs of choice suggest that the benefits of mate choice may sometimes be very small. Future laboratory studies should provide more realistic choice scenarios. Many laboratory studies allow females simultaneously to assess two or more males. In the field, sampling is usually sequential and this may yield very different results because of memory retention (and interference and transference, see Papaj & Lewis, 1994) and sampling costs.

Although we have not dealt in any detail with the neurobiology or psychology of female choice, we suggest that this may also be a profitable area of research (reviewed by W. Eberhard & W. Wcislo, in preparation). The general process of choice has been extensively studied by psychologists and there is a large literature on such topics as discrimination, learning, and memory retention, transference and interference. Most models of mate choice have not considered these more proximate factors. This is sometimes a problem as it may lead to unrealistic claims about what females are capable of doing. A simple point worth keeping in mind is that most animals make many choices about foraging every day but only rarely regarding mating. We might therefore expect investment in the sensory apparatus and processing facilities used in feeding to be more developed than in those used in mating. The degree of misfit between predicted and observed choices generated by 'optimal foraging' models may therefore be far smaller than that derived from 'optimal mate choice' models. Of course, this argument is affected by whether or not the rewards from the correct choice are higher for mating than feeding decisions. Many would argue that the rewards from mate choice are high. However, the small number of males sampled by females in many species (often the first male encountered is accepted: see Section IX. 1) and the reduction in choosiness in response to small increases in costs (see Sections VI. 1 & 2, Section VII. 5) are tantalizing pieces of evidence that this is not always the case. Mate choice for indirect benefits may have dramatically beneficial effects in some species (e.g. Norris, 1993; Petrie 1994), but this is not always the case (e.g. Nicoletto, 1995).

Variation among females in reproductive success may be smaller than that among males (Clutton-Brock, 1988); however, from a functional perspective this does not make it any less important. For those interested in the identification of adaptations and constraints on optimality, female mate choice and female manipulation of males is a relatively unexplored area. The wealth of opportunities is illustrated by the fact that we deliberately avoided reviewing variation among females in relation to multiple mating and sperm competition. Very little is known about the extent to which females control sperm competition (Barnett, Telford & Tibbles, 1995), let alone the effect of variation in morphological, physiological and behavioural traits that influence sperm competition or the opportunity for multiple matings. The recent publication dates for much of the research we have cited indicates an increasing interest in the extent to which females are active participants in sexual selection. There are exciting research opportunities ahead for those so inclined.

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