J. evol. Biol. 8: 129–171 (1995)

1010–061X/95/020129–43 $ 1.50 + 0.20/0

Mini-review

The genetic basis of female mate preferences

Theo C. M. Bakker[1] and Andrew Pomiankowski[2]

[1]*Abteilung Verhaltensökologie, Zoologisches Institut, University of Bern, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland*
[2]*Department of Genetics and Biometry, University College of London, 4 Stephenson Way, London NW1 2HE, U.K.*

Key words: Sexual selection; female mating preference; genetic variance; genetic covariance.

Abstract

We review the evidence for genetic variation in female and male mate preferences. Genetic differences between species and partially isolated races show that preferences can evolve and were genetically variable in the past. Within populations there is good evidence of genetic variation, both of discrete genetic effects (8 cases) and quantitative genetic effects (17 cases), from a diverse range of taxa. We also review evidence for the presence of genetic covariance between mate preferences and sexual traits in the other sex. The 11 studies go a long way to validating the theoretical prediction of positive genetic covariance. The few negative results are best explained by a lack of appropriate experimental design. One unresolved question is whether genetic covariance is due to linkage disequilibrium between unlinked genes or physical linkage. Some evidence points to linkage disequilibrium but this is not yet conclusive.

Introduction

Biologists have taken a long time to recognise that female mate preferences evolve adaptively and are the major cause of diversity and elaboration in male sexual traits. But even today there is resistance to Darwin and Fisher's theory of sexual selection. It is frequently claimed that there is little or no genetic variance in female preference (Paterson, 1985; Boake, 1989). If true, this must severely limit the evolutionary potential of mate preferences. A lack of genetic variation in

preference will also restrict the build up of genetic covariance with genes for male sexual traits. In the absence of genetic covariance, Fisher's runaway and the good genes process cannot act as forces maintaining female preference. This negative view gives credence to the proposal that female preferences do not coevolve with male sexual signals, rather only the male trait evolves to "exploit" pre-existing "sensory bias" (Ryan et al., 1990).

But is there any reason to believe that mate preference is a trait different from any other, lacking genetic variation? The argument put forward has two complementing facets. First, it is claimed that individual females in repeat trials are often inconsistent in their mate choice, suggestive of a large component of environmental variance (Boake, 1989). However, high repeatability has been found in several studies (Moore, 1989; Bakker, 1993; Møller, 1994; Godin and Dugatkin, in press). Also, heritability can often be a misleading indicator of the ability of a trait to evolve. What is more important is the level of additive genetic variance (Houle, 1992). Behavioural traits in general have low heritabilities but they are not typified by low levels of additive genetic variance (Houle, 1992; Messina, 1994).

A second line of argument is that mate choice and mating sexual signals evolve in a coordinated fashion under strong stabilising selection that results in a reduction in genetic variation in mean preference and in the "window of response" (Paterson, 1985). All traits subject to selection are expected to suffer short term reductions in genetic variation. But we are interested in the long term balance between this loss and other forces like mutation, migration and changes in the direction of selection that maintain genetic variation. Other traits subject to stabilising selection retain significant genetic variation (e.g., van Noordwijk et al., 1988; Houle, 1992). In addition, many preferences have directional rather than stabilising effects on mate choice. It is not obvious whether there will be strong pressure for reduced genetic variation in this case. This is a complicated matter and not one we intend to discuss here, except to note that there is no compelling reason why preference is a trait that should have particularly low genetic variation.

Our approach to this debate is to avoid theoretical arguments by going straight to the empirical data. The central message of our review is that there is abundant evidence of genetic variation in mate preferences. For a long time it has been known that there is genetic variation between species (Butlin and Ritchie, 1989). Often hybrids show intermediate levels of preference. But this merely establishes that there was genetic variation in the past and this has contributed to evolutionary divergence. Intraspecific studies, preferably of geographically continuous populations, are needed. There are now many studies at this level which suggest that preference is a genetically variable trait.

The data for genetic covariance between female mating preference and male traits is more recent but equally compelling. Though the evidence is not unequivocal, in our view most of the failures to demonstrate genetic covariances reflect insensitivity of the experimental design. Genetic covariances in sexual selection (Pomiankowski, 1988) are thought to arise through linkage disequilibrium between unlinked loci rather than physical linkage (restrictions on the recombination rate). If normal mate choice is disrupted, genetic covariance in an experimental population will decline quickly. The rate of decay for unlinked genes is 50% per generation. So it

may only be possible to detect genetic covariances during the first couple of generations of an experiment. This limitation seems to have been overlooked in a number of experiments. However, we should not assume that demonstrations of genetic covariance are necessarily due to linkage disequilibrium between unlinked genes. This must be tested. Unfortunately, none of the recent examples of positive genetic covariances between preference and preferred traits have done this, so this matter remains unresolved.

Models of sexual selection presume that genetic covariance arises because females with the most extreme mate preferences mate more frequently with males bearing the most exaggerated sexual traits. Fisher (1930) was the first to realise that the evolution of female preference will be promoted by this genetic covariance. Selection for the male sexual trait will cause a proportionate increase in female preference and both traits will increase together in a runaway. This has led some to suppose that a demonstration of genetic covariance is evidence for Fisher's runaway (Moore, 1989; Johnson et al., 1993). This is not the case. A similar genetic association is also predicted by good genes (i.e., handicap) models (Pomiankowski, 1988). In the handicap process females with stronger preferences are again predicted to mate with more exaggerated males generating linkage disequilibrium between genes for preference and those for the male trait. But in this case the genes that alter expression of the male trait are assumed to have their primary effects on other traits which affect viability. So both of these theories predict genetic covariances. The prime way to distinguish between them is to look at the effect of mate choice on offspring fitness which increases male mating success (Fisher's runaway) and/or male and female survival (good genes).

Theoretical estimates of the level of genetic covariance expected have recently been made (Barton and Turelli, 1991; Pomiankowski and Iwasa, 1993; Iwasa and Pomiankowski, in press). The exact calculation is complex but under a number of general and non-restrictive assumptions a surprisingly simple approximation is given by,

$$B \approx aG_pG_t\,. \tag{1}$$

B, the equilibrium genetic covariance, clearly depends on there being genetic variance in female preference, G_p, and in the male sexual trait, G_t. The level of covariance is principally determined by a, the effectiveness of female preference and male signalling in creating non-random mating. It does not strongly depend on natural selection on choice or on the male trait. Neither does it depend on physical linkage between genes for preference and the male trait because recombination symmetrically effects the build up and break down of covariance. Equation (1) holds both for the Fisher's process (Pomiankowski and Iwasa, 1993) and for good genes selection (Iwasa and Pomiankowski, in press). It indicates that though the genetic covariance may be small it is likely to be a measurable quantity (similar order to genetic variances) if there are good opportunities for non-random mating.

Two caveats to the review should be noted. In this introduction and elsewhere we have written as if the male is the signaller and the female is the chooser. This is not always the case and there are some well known examples of sex-role reversal

(Vincent et al., 1992). We will discuss several cases, in particular male preference for female pheromones in butterflies and moths. Second, we have restricted our review to the genetics of mate preference in higher animals. There is an extensive literature on mate choice in plants. In addition, many micro-organisms use signalling in their mating behaviour. Both of these areas deserve attention in the future.

How to measure genetic variation and covariation?

We would like to know whether there is additive genetic variance in mate preferences and additive genetic covariance between preferences and sexual traits. We would also like to know the heritability of preferences in natural populations. Measuring these parameters is in principle straightforward. Additive genetic variation can be computed from the resemblance between related individuals, after excluding other non-genetic and non-additive sources of resemblance (Falconer, 1989). The most frequently used comparisons are parent-offspring, full-sib and half-sib. These measures can be extended by computing the realised heritability using artificial, directional selection. Genetic covariation can be estimated from the same data-sets used to measure genetic variation (Falconer, 1989).

To get reliable genetic estimates, animals need to be bred under standardised environmental conditions. Control is often gained by collecting individuals from the wild and breeding them under laboratory conditions. But this can potentially lead to the loss or generation of variation not present under natural conditions. It must be remembered that genetic parameters are not intrinsic properties of individuals but contingent properties of populations living under particular environmental conditions. Laboratory studies are good at revealing whether genetic variation is present but they can not substitute for field studies to measure genetic parameters in the wild. A productive half way house is manipulations on natural populations that control some important environmental variables, for example egg-swapping to control for parental care (Norris, 1993). All the genetic studies reported here have been carried out, at best, in semi-natural laboratory conditions. The reliability of these estimates of additive genetic variance depends on the number of families and the number of offspring per family analysed. Often sample sizes are small. This places limits on the discovery of natural genetic variation because fairly large numbers of individuals are needed relative to phenotypic studies (Bakker, 1994).

In several cases, parent-offspring comparisons have been augmented by artificial selection experiments. Individuals at one extreme of the distribution of phenotypes are taken as parents for the next generation and this procedure is repeated for several generations. Artificial selection provides the most unambiguous evidence for the contribution of additive genetic variation to the phenotypic variation. In addition, it produces phenotypes that can be used for further study of sexual selection. Selection experiments must guard against an apparent response to selection due to random genetic drift caused by few individuals being chosen to be parents for the succeeding generation (Henderson, 1989). Replicated selection lines control for drift effects. Bidirectional or two way selection is more informative and

more effective than is unidirectional selection (Hill, 1972b). An unselected control line will enable the assessment of asymmetry between the responses in upward and downward directions (Falconer, 1989).

Instead of measuring one character (mate preference), two characters (preference and sexual trait) must be measured to demonstrate the existence of genetic covariation. The same techniques of comparing parents and offspring are applicable. The numbers needed to achieve reliable estimates are higher than in the case of genetic variation because the standard errors of the two heritability estimates are important in determining the standard error of the genetic correlation (Falconer, 1989). Estimating genetic correlations from selection experiments is possible as well. Again replicate selection lines are needed to control for spurious associations that may arise from drift (Henderson, 1989). Usually it is necessary to know the heritabilities of the two traits. A way to circumvent this demand is to set up a double selection experiment (formula 19.7 in Falconer, 1989), selecting on preference in one set and on the sexual trait in a second (Bakker, 1994). In the first set the correlated response in the sexual trait is scored while in the other set correlated changes in preference are scored.

The nature of genetic correlations in sexual selection makes artificial selection a rather risky method (Bakker, 1994; Heisler, 1994). Associations between genes for male sexual traits and genes for female preferences build up through mate choice causing non-random associations between genes in progeny (i.e., linkage disequilibrium). This genetic correlation will be maintained in an experiment as long as females exert the same strength of preference as they do in the wild. If mate choice is restricted, linkage disequilibrium will decay. Under random mating the rate of decline is proportional to the rate of recombination; the genetic correlation being reduced by half every generation for unlinked genes under random mating. This is not a grave problem for laboratory investigations of parent-offspring or sib correlations using wild caught individuals as these take place over a single generation. But it is a problem if the culture of animals prior to experimentation in any way interferes with normal mate choice. Recombination is also a problem for selection experiments in the lab carried on for more than one or two generations. By their nature, selection experiments pick certain individuals (male or female) to parent the next generation and this will restrict mate choice. Only by using large numbers and allowing choice amongst selected individuals will there be a chance of maintaining linkage disequilibrium. If linkage disequilibrium declines during the selection experiment most of the correlated response will take place in the first few generations, with subsequent generations merely contributing noise.

Another potential cause of genetic correlations between preference and sexual trait is pleiotropy. At first glance this seems an unlikely cause of correlations as mate preference and sexual trait are such distinct characters that are unlikely to be under the same genetic control. For example, it appears implausible that genes for the auditory system of a frog (preference) might contribute to call characteristics (sexual trait) or vice versa. However, there are two reasons why pleiotropy cannot be so easily dismissed. First, there is the concept of genetic coupling, the possibility that similar neural mechanisms control signal production and reception (Alexander,

1962). Though there is very little evidence for coupling, there are some systems which are plausible examples from a physiological viewpoint (Butlin and Ritchie, 1989; Boake, 1991). Second, pleiotropy could arise because of similar condition dependent expression of preference and sexual traits. Condition dependence is common in secondary sexual traits (Andersson, 1994) and there is some evidence for condition dependent choice as well (Slagsvold et al., 1988; Milinski and Bakker, 1992). As condition is likely to have a strong genetic basis, genes for condition might easily cause pleiotropic effects on both traits.

It will be clear that the application of genetic methods to study sexual selection is limited. Besides the demands of the breeding designs, one must have the availability of an experimental system in which the male trait preferred by females is known and in which reliable quantification is possible of both preference and sexual trait. A preliminary repeatability analysis of the traits can reveal whether the system is suitable for further analysis (repeatability gives a maximum estimate of heritability; Boake, 1989; Falconer, 1989). If females are not consistent in their choices, there will be little point searching for genetic influences. Confounding influences are numerous and need to be eliminated. They depend on the organism used. Some potential influences on preferences are maternal effects due to cytoplasmic genes or common environment, paternal effects in the case of internal fertilisation or paternal care (Bakker, 1993), changes in female investment with mate sexual trait size (Burley, 1988; Petrie and Williams, 1993), effects of density and diet on male traits and preferences (Alatalo et al., 1988) and even the effect of anaesthetics on preferences (Joachim and Curtsinger, 1990).

In spite of these potential problems in carrying out genetic analysis with less standard organisms (i.e., not *Drosophila* or mouse), genetic studies of mate preferences are accumulating. Arnold's (1983) advocacy of genetic studies more than 10 years ago has been fulfilled. It now seems appropriate to survey the state of knowledge.

Additive genetic variance in mate preference

For almost ten years, the ladybird *Adalia bipunctata* provided the best example of a female choice gene (Majerus et al., 1982, 1986). Selection experiments appeared to show the presence of a single, dominant gene causing strong preference for melanic males, with the frequency of this gene varying between populations. However, attempts to repeat the experiments failed (Kearns et al., 1992). Females from the original selection experiment were found to mate at random one generation later and new isofemale lines failed to demonstrate genetic variation in preference. Though these new results have been questioned (O'Donald and Majerus, 1992), the ladybird can now be counted only as a possible example of a female choice gene. The loss of this classical example was unexpected but the gap has been more than filled by the recent accumulation of examples for other species.

One can search for the existence of genetic variation in female mating preference at different levels: interspecific, racial or within populations. Differences between

species and their hybrids was the main topic of interest before the boom in studies of sexual selection in the 1980s shifted attention to the evolution of mating preferences within populations. Species comparisons show whether female preferences have evolved and potentially might be important in mapping preference genes (e.g., Grula and Taylor, 1980; Zouros, 1981). But interspecific studies are not informative about the presence of additive genetic variation within populations. We have therefore left such studies out of the present review.

Comparisons of racial or strain differences suffer from the same restrictions but to a lesser degree. If races are only partially isolated then migration will maintain some degree of variation within races and hence some ability to respond to selection or to harbour covariation. For these reasons we have considered cases where semi-isolated populations of the same species have been analysed for genetic differences in preferences (Tab. 1).

The main source of information comes from intraspecific studies. These have been split into cases where there are discrete genetic effects and those with quantitative genetic variance in preferences (Tab. 2). Additive genetic variance has been identified from parent-offspring or sib correlations (cockroach, pink bollworm, redbanded leafroller), chromosomal inversions or linkage to obvious phenotypic polymorphisms (mouse, seaweed fly, sulfur butterfly), isofemale lines (brown planthopper), selection on female preferences or male sexual traits (field grasshopper, fruit fly, guppy, ladybird, pink bollworm, planthoppers, stalk-eyed fly, stickleback), analysis of mutants (fruit fly) or evidence of evolutionary change (fruitfly, melon fly).

Population differences

The most obvious examples of genetic variance in mating preference are in species where male sexual traits vary geographically. In several cases it has now been established that females show a concomitant shift in their mating preferences as well. For example, in the bushcricket *Ephippiger ephippiger*, there is great variation in male song between populations, forming monosyllabic and polysyllabic song races (Ritchie, 1991). Investigation of female mate choice under controlled laboratory conditions with synthetic songs reveals that females show strong preferences for male songs from their native population (Ritchie, 1991). The genetic basis of these differences has been shown in crosses between races (Ritchie, 1992). Hybrid male song is intermediate as is hybrid female preference.

A similar pattern occurs in the two pheromone races of the European corn borer *Ostrina nubilalis*. This provides a well documented case of single gene effects on mate preferences (Klun et al., 1973). There are two components in the female pheromone that are attractive to males. Females of the two strains produce opposite blends of the two compounds (Z and E); in the E-strain the blend is a 3:97 molar mixture (Z:E), whereas in the Z-strain the ratio is 97:3. Natural hybridisation between strains occurs at low frequency in sympatry but in the laboratory it is readily achieved and produces viable and fertile offspring. Mende-

Table 1. Genetic variation in mating preference and covariation with preferred trait: population (strain, racial) differences.

Organism	Preferred trait (male unless stated)	Level of comparison	Reference
Insects			
bushcricket *Ephippiger ephippiger*	song syllable number	song races	Ritchie, 1991, 1992
European corn borer *Ostrina nubilalis*	female pheromone blend	pheromonal strains	Klun et al., 1973 Hansson et al., 1987 Roelofs et al., 1987 Löfstedt et al., 1989
turnip moth *Agrotis segetum*	female pheromone blend	populations	Löfstedt et al., 1986 Hansson et al., 1990 Löfstedt, 1993
fruitfly *Drosophila pseudoobscura*	unknown	lab strains of different age	Millar and Lambert, 1986
Fishes			
guppy *Poecilia reticulata*	relative orange area	populations	Breden & Stoner, 1987 Houde, 1988 Stoner & Breden, 1988 Houde & Endler, 1990
guppy *Poecilia reticulata*	conspicuousness (courtship and coloration)	populations	Luyten & Liley, 1991
Amphibians			
cricket frog *Acris crepitans*	call frequency	populations	Capranica et al., 1973 Nevo & Capranica, 1985 Ryan & Wilczynski, 1988 Ryan et al., 1992 Wilczynski et al., 1992
Birds			
house finch *Carpodacus mexicanus frontalis*	brightness of coloration	populations	Hill, 1994

lian crosses (F1, F2, backcrosses) between the two strains were screened for female pheromone production, male olfactory receptor cell response to pheromone mixtures and male behavioural responses to pheromone mixtures in a flight tunnel (Roelofs et al., 1987; Löfstedt et al., 1989). Female pheromone blend is primarily controlled by a single autosomal gene and the behavioural response to pheromone is coded by a sex-linked gene. By appropriate crossing one can thus breed male

Variation in preference	Crosses intermediate	Covariation	Comment
yes	yes	+ive	preference gene(s) autosomal; monosyllabic and polysyllabic song races
yes	yes	+ive	3 genes involved: one autosomal for pheromone blend, one Z-linked for response behaviour, and one autosomal for receptors
yes	not studied	+ive	gross covariation between pheromone blend and receptor types
yes	not studied	+ive	assortative mating in some combinations of old lab stocks and recently collected flies; may be due to evolution of preference in the lab
yes	not studied	+ive	populations differ in strength of preference for orange area
yes	not studied	+ive	assortative mating in mixtures of wild-caught males and females from two populations
yes	not studied	+ive	female auditory tuning and male dominant call frequency covary on fine and large scales
small (NS)	not studied	weak +ive (NS)	no genetic variation in male signal (Hill, 1993)

NS = not significant.

moths that possess E-type antennae but respond as Z-type males with no response to the E source.

Several other studies have documented variation in female preferences that geographically covary with male sexual traits. In the guppy *Poecilia reticulata*, the strength of female preference for male orange area varies across river basins and between lower and upper regions of streams (Breden and Stoner, 1987; Houde and

Table 2a. Genetic variation in mating preference: discrete genetic effects.

Organism	Preferred trait (males unless stated)	Reference
Insects		
fruitfly *Drosophila melanogaster*	mutants for eye colour (*w*, white or w^a, white apricot)	Tebb & Thoday, 1956
fruitfly *D. melanogaster*	body colour mutant (*yellow*) with abnormal courtship	Dow, 1977
fruitfly *D. melanogaster*	body colour mutant (*y*, yellow) with abnormal courtship	Heisler, 1984
fruitfly *D. melanogaster*	cuticular hydrocarbons	Scott, 1994
seaweed fly *Coelopa frigida*	traits associated with alcohol dehydrogenase (*Adh*) locus	Engelhard et al., 1989
seaweed fly *C. frigida*	body size associated with inversion karyotype	Gilburn et al., 1992, 1993 Gilburn & Day, 1994
sulfur butterfly *Colias eurytheme*	pheromone blend	Sappington & Taylor, 1990
two-spot ladybird *Adalia bipunctata*	elytra colour	Majerus et al., 1986 Kearns et al., 1992 O'Donald & Majerus, 1992
Mammals		
house mouse *Mus domesticus*	odours associated with *t*-complex genotype	Lenington et al., 1988, 1992 Coopersmith & Lenington, 1990 Williams & Lenington, 1993

Endler, 1990). To a large extent, male colour patterns track differences in female preferences (Houde and Endler, 1990), though there are exceptions (Houde, pers. comm.). In some streams, other male traits are used by females in their mate choice, for example body size (Reynolds and Gross, 1992). Cricket frogs, *Acris crepitans*, from New Jersey and South Dakota show correlated differences in the dominant frequency of the male's call and the frequency tuning of the female's auditory system (Capranica et al., 1973; Nevo and Capranica, 1985). These differences in part relate to a cline in body size. But there is evidence for covariation in male call frequency and female auditory tuning on a local scale in frogs from two sides of Texas when body size variation is controlled for (Ryan and Wilczynski, 1988; Ryan

Genetical method	Preference gene(s)
effect of mutant on female preference	white locus
one way selection for male mating success and female receptivity; selected lines backcrossed on parents	increase in female acceptance of mutant males, probably by a reduction in choosiness; additive & dominant autosomal, sex linked and maternal genetic effects (see Heisler, 1984)
crosses between lab strains differing in preference	*X*-linked and autosomal genes implicated in causing increased mating frequency with yellow mutant; preference is not due to difference in willingness of female to mate
crosses between lab strains differing in preference	Canton-S females discriminate in favour of their own males, Tai-Y females do not and this preference maps to gene(s) on chromosome 3
correlation of preference with *Adh* alleles	*Adh* locus linked to the $\alpha\beta$ inversion; B and D alleles associated with choosy females, C allele associated with random mating
correlation of preference with inversion karyotype	preference linked to inversion
correlation of preference with female colour morphs	linked gene or pleiotropic effect of alba/orange sex limited wing pigment gene
selection for preference and isofemale lines	dominant gene but not confirmed by subsequent study
correlation of preference with *t*-complex inversion	*t*-complex; *t* heterozygous females prefer wildtype males; *t* homozygotes are sterile or inviable

et al., 1992). A study of laboratory strains of *Drosophila pseudoobscura* has reported several cases of assortative mating (in 3 out of 7 combinations). All cases of assortative mating are between strains of different geographical origin. In two cases, females of the new stock discriminate against males of the old stock, while old stock females accept both males. This difference may be due to evolution of female preference in the lab (Millar and Lambert, 1986). Finally, females of the turnip moth, *Agrotis segetum*, produce a pheromone consisting of a mixture of three acetates. There is great variation in pheromone composition within and between population. Pheromones from Western European populations differ from those produced by females in Eastern Europe and Western Asia. This pattern is mirrored

Table 2b. Genetic variation in mating preference: quantitative genetic effects.

Organism	Preferred trait (male unless stated)	Reference
Insects		
brown planthopper *Nilaparvata lugens*	call (pulse repetition frequency)	Butlin, 1993a
cockroach *Nauphoeta cinerea*	olfactory cues related to dominance	Moore, 1989
common field grasshopper *Chorthippus brunneus*	call (mean syllable length)	Charalambous et al., 1994
fruitfly *Drosophila melanogaster*	song (experimentally reduced wings)	Cook, 1973
fruitfly *D. melanogaster*	mutants for body colour (*e*, ebony) or reduced wings (*vg*, vestigial)	Crossley, 1974
fruitfly *D. melanogaster*	artificial male song varying in cycle rhythm	Greenacre et al., 1993
fruitfly *D. mercatorum*	call (interpulse interval)	Ikeda and Maruo, 1982
fruitfly *D. mojavensis*	unknown	Koepfer, 1987
fruitfly *D. montana*	song (experimentally reduced wings)	Aspi, 1992
pink bollworm *Pectinophora gossypiella*	a) female pheromone titre	Collins & Cardé, 1990
		Collins & Cardé, 1989a
	b) female pheromone blend	Collins & Cardé, 1989b
melon fly *Dacus cucurbitae*	unknown	Hibino and Iwahashi, 1991
planthopper *Ribautodelphax imitans*	female call (interpulse interval)	De Winter, 1992

Genetical method	Heritability ± SE	Comment
isofemale lines	no estimate: preference (NS) preference window (*)	isofemale lines differ significantly in strength of preference but not in mean pulse repetition frequency preferred
a) repeatability b) indirect (father-daughter)	no estimate (*) no estimate (*)	see Table 3
two way selection for preference	no estimate (*) and (NS)	marked divergence between lines in first generation; problem that selection was for female responsiveness as well as preference
one way selection for mating speed	no estimate (*)	selection increased % of females receptive, shortened courtship duration and increased latency to courtship
selection for assortative mating	no estimate (*)	selection increased female repulsion of heterogamic males and the frequency of homogamic matings
song playback to females with *per* (period) locus mutants	no estimate (*) and (NS)	females from an old mutant *per* stock show no discrimination against mutant song unlike more recently established mutant stock
indirect (correlated response to two way selection for male IPI)	no estimate (*)	see Table 3
selection for assortative mating	no estimate (*)	selection increased Sonora female mate preference for their own males
one way selection for acceptance rate	F1 0.104 ± 0.286 (NS) F2 0.518 ± 0.243 (*)	heritability estimate significant for a threshold, polygenic model of female choice
one way selection for male response (wing fanning)	0.16 ± 0.02 (*)	significant heritability from selection of male response to a 65% ZE blend
parent-offspring	0.38 ± 0.11 (*)	P-O regression gave significant heritability for response to 25% and 44% ZE blend but not to 65% ZE blend (44% is average)
indirect (correlated response to two way selection for female pheromone)	no estimate (*)	see Table 3
sterile male release over many years	no estimate (*)	females in populations exposed to sterile males now discriminate against mass reared males
indirect (correlated response in male preference to two way selection for female IPI)	no estimate (*) and (NS)	see Table 3

Table 2b. (continued).

Organism	Preferred trait (male unless stated)	Reference
redbanded leafroller *Argyrotaenia velutinana*	female pheromone blend	Roelofs et al., 1986
red flour beetle *Tribolium castaneum*	pheromone	Boake, 1989
stalk-eyed fly *Cyrtodiopsis dalmanni*	relative eye span	Wilkinson & Reillo, 1994
Fishes		
guppy *Poecilia reticulata*	relative orange area	Houde, 1994
guppy *Poecilia reticulata*	total coloration	Godin and Dugatkin, in press
three-spined stickleback *Gasterosteus aculeatus*	intensity of red breeding coloration	Bakker, 1993
Birds		
red jungle fowl *Gallus gallus*	various colour and size traits	Johnson et al., 1993
barn swallow *Hirundo rustica*	tail length	Banbura, 1992 Møller, 1994

by the relative frequency of receptor cells on male antennae tuned to the three components (Löfstedt et al., 1986; Hansson et al., 1990; Löfstedt, 1993). Males also show coincident differences in attraction to baits supplemented with the different pheromone components (Hansson et al., 1990).

This is not an exhaustive list of population level variation in mate preferences and sexual traits (reviewed in Butlin, in press). However, few cases have been investigated in great depth. In all the cases listed above it seems likely that geographic differences have a genetic basis. But in only two cases is there good evidence that genetic differences underlie mate preference variation (bushcrickets and European corn borer). A further example acts as a caution to the view that genetic variance in female preference is necessarily present where sexual traits vary geographically. Within house finch populations, male carotenoid plumage coloration varies from pale yellow to bright red (Hill, 1991). Mean male coloration varies greatly between populations. However, the mean female preference differs

Genetical method	Heritability ± SE	Comment
father-son	0.41 (*)	strong preference for high %E pheromone in sons of fathers with strong preference high and mothers that produce high %E pheromone
repeatability	no estimate (NS)	female preferences vary greatly between days, suggesting heritability is very low
indirect (correlated response to two way selection for male trait)	no estimate (*) and (NS)	see Table 3
indirect (correlated response to two way selection for male trait)	no estimate (*)	see Table 3
repeatability	0.58 ± 0.11 (*)	most females preferred bright males but some preferred drab males
a) repeatability b) full-sib/half-sib c) full-sib d) indirect (brother-sister)	0.65 ± 0.14 (*) no estimate (*) 0.43 ± 0.37 (NS) no estimate (*)	estimates based on 6 extreme males mated to 14 random females
mother-daughter	no estimate (NS)	inbred population
a) repeatability of choice for absolute tail length b) repeatability of choice for rank of tail length	0.15 ± 0.23 (NS) 0.18 ± 0.16 (NS) 0.57 ± 0.11 (*)	field data, so consistency of choice between years may be environmental (e.g. caused by consistent differences in female condition) rather than genetical

NS = $p > 0.05$; * = $p < 0.05$.

only slightly; females from all populations prefer the most brightly coloured males (Hill, 1994). The lack of variance in female preference might be due to the high environmental variability of coloration. Males from different populations fed carotenoid-deficient or carotenoid-rich diets do not differ in appearance (Hill, 1993). This may have constrained local differentiation of preferences.

Within population differences

Discrete genetic variation

The literature on genetical studies of mating preference within populations revealed no less than 8 examples of discrete genetic effects (Tab. 2a) and 17 examples of quantitative genetic effects (Tab. 2b). We include in the discrete genetic

variation category examples where crude mapping has been attempted indicating the location of the mate preference gene(s). Insects have been most intensively studied (20 out of 25 studies) for obvious reasons: short generation times, ease of housing and rearing. Higher phyla are under represented which is a pity in view of the many good examples of female choice in birds. A range of secondary sexual traits have been investigated including song, odour and coloration. These traits can be reliably quantified.

In many cases preferences for these traits have been experimentally demonstrated using simultaneous choice tests. Members of the choosy sex are allowed to select between two potential mates or between two natural or synthetic signals. Not all studies mentioned have experimentally identified the preferred character. In some systems it is very difficult to manipulate the male sexual trait and it remains unclear whether females discriminate between males using this trait or use another associated trait. Knowledge of the exact criterion of choice allows greater sensitivity in the genetic analysis but is not essential.

The best examples of discrete genetic effects on female preference have exploited obvious phenotypic polymorphisms in male sexual signals. In two cases these are associated with chromosomal inversions (mouse, seaweed fly) and in another two with body colour dimorphism (ladybird, sulfur butterfly).

The *t*-complex in the house mice *Mus domesticus* and *M. musculus* is a nice example of good genes sexual selection. Around 10–20% of wild mice carry the *t*-complex inversion on chromosome 17 (Hammer, 1991). Males homozygous for *t* are always sterile and suffer early lethality when both *t* chromosomes are from the same complementation group (*t* haplotypes carry deleterious recessives). The *t*-complex has no influence on female fertility or viability. Thus matings with males heterozygous for *t* can have severe fitness consequences for females. Female preference has been tested using simultaneous choice tests in which females were offered male urinary odours or inaccessible live males with $+/+$ and $+/t$ genotypes. Wild-type females showed no preference but females heterozygous for *t* preferred wild-type males when in oestrous (Lenington et al., 1988, 1992; Williams and Lenington, 1993). Further choice tests with females carrying *t* haplotypes of different complementation groups suggest that females discriminate between complementation groups and prefer males with dissimilar *t* haplotypes (Coopersmith and Lenington, 1990). Despite strong natural and sexual selection against *t* haplotypes, they are maintained at high frequency because meiotic drive causing the *t* haplotype to be transmitted to about 95% of the offspring of heterozygous males (Hammer, 1991). In addition, males heterozygous for *t* are more aggressive than wild-type males which may give them a selective advantage in competitive situations (Lenington, 1991).

It is unclear how many choice genes are present in the *t*-complex or exactly where they are located. The *t*-complex is a large chromosome segment linked by 4 inversions (Lyon, 1991). The MHC (major histocompatibility complex) lies within the *t*-complex and itself might be the cause of preferential mating. The *t* complementation groups used by Coopersmith and Lenington (1990) are each associated with a specific MHC-haplotype. Thus female preference for males with dissimilar *t*

haplotypes (Coopersmith and Lenington, 1990) may be MHC-based. Although inversions within the *t*-complex suppresses recombination in $+/t$ mice, recombination occurs at normal rates in compound heterozygous females (those with two *t* haplotypes from different complementation groups). It is thus possible to select mice with MHC haplotypes characteristic of *t*-bearing chromosomes which have two or no lethal factors, that must have undergone recombination in the *t* region (Lenington et al., 1988, 1992). Female preference of mice that are identical at the MHC but carry either two or no lethal factors differed significantly suggesting that preferences for *t* haplotypes are independent of the MHC (Lenington et al., 1988, 1992). Preliminary mapping indicates that there are several female preference genes that map to different regions of the *t*-complex (Lenington, 1993).

The MHC might seem to provide a second example of female choice genes in the mouse. The MHC is highly polymorphic and strongly influences individual odours. Several studies have documented that females prefer males that carry a MHC type different from their own (Yamazaki et al., 1976, 1988; Egid and Brown, 1989; Potts et al., 1991). MHC based disassortative mating reduces the incidence of matings with close relatives and hence of inbreeding (Potts and Wakeland, 1993). It may also serve to improve resistance to infectious disease by increasing the proportion of MHC heterozygotes produced (Potts and Wakeland, 1993). Despite the strong mating preferences based on urinary odours associated with the MHC, we did not include the MHC-based preferences in our list of discrete genetic effects on variation in mating preferences (Tab. 2b). There is no evidence for genetic variation in MHC based preferences. Female mating preferences are probably generated by imprinting on parental MHC derived smells, that are then avoided when choosing a mate. This view is supported by cross-fostering experiments in mice. Male mice homozygous for one MHC haplotype avoid females with self MHC as mates. But when cross fostered by parents homozygous for another MHC haplotype, their preference is reversed and they prefer females with their own MHC haplotype (Yamazaki et al., 1988). Unfortunately, no such experiments have been done with female preferences.

Obvious genetic variation caused by an inversion has been used to uncover genetic variation in the seaweed fly, *Coelopa frigida* (Engelhard et al., 1989; Gilburn et al., 1992, 1993; Gilburn and Day, 1994). Seaweed flies have a large polymorphic inversion (two forms, α and β) that causes strong heterosis. The alcohol dehydrogenase gene *Adh* is located in the inversion and three alleles are known to be associated with female mate choice. Females with the *Adh*-C allele exhibit no mate discrimination whereas females with *Adh*-B or *Adh*-D mate non-randomly (Engelhard et al., 1989). Further study of this system has revealed genetic variance in female preference for male size and genotype within populations which we will discuss further in the section on genetic covariation (Gilburn et al., 1992, 1993; Gilburn and Day, 1994). In neither case is it known whether there is one or several female choice genes within the inversion.

Two other studies provide less concrete evidence of discrete genetic effects on mating preferences. We have already mentioned studies by Majerus, O'Donald and co-workers on the ladybird *Adalia bipunctata*. At the moment we can only offer this

as an unconfirmed example of a single gene controlling preference for melanic males. In the sulfur butterfly *Colias eurytheme*, there is some evidence that female mate preference is associated with a female sex-limited colour dimorphism (Sappington and Taylor, 1990). The amount and mixture (3 components) of pheromone produced by male *C. eurytheme* is variable both within and between populations. Mating success of males at one extreme of the character distribution was much higher with alba females, whereas that of males at the opposite extreme was much higher with orange females. The most likely explanation for this difference in female mate choice is that alba and orange females differ physiologically which alters their threshold for responding to pheromone (Sappington and Taylor, 1990). Genetic variance in female mate choice thus arises as a side-effect of selection maintaining the female colour dimorphism.

In addition to these cases, there have been several investigations in *Drosophila melanogaster*. The most convincing is Heisler's (1984) study of female preference using *yellow*, a body colour mutant with abnormal courtship. A survey of lab strains showed that there is high variance in the propensity of females to accept *yellow* males. To uncover the genetic basis of this variability, crosses were made between two lab strains, one which rarely mated with *yellow* males (NB), the other which frequently mated with *yellow* males (MC). The stronger preference in the MC strain was in part due to greater female receptivity to any male as previously suggested by Dow (1977). But MC females also mate at a higher rate with *yellow* males in competition with wildtype males. The difference between strains is controlled by at least two loci, a recessive *X* linked element and an autosomal element that shows overdominance. There is also some evidence of coevolution. Low receptivity in NB females is matched by NB males being slow maters, whereas the high receptivity of MC males is matched by quick mating in MC males.

Scott (1994) using a similar analysis has reported a different preference system based on male cuticular hydrocarbons. Canton-S females mate more quickly with their own males than with males of Tai-Y and Florida-9 strains, whereas Tai-Y females do not show any discrimination. These strains differ in their chemical cues. The hydrocarbon profile of Canton-S males consists primarily of 7-tricosene, whereas Tai-Y males produce primarily 7-pentacosene and Florida-9 is intermediate. The difference between the strains was genetically investigated by crossing which showed that the main effect mapped to the Canton-S third chromosome.

What is less clear from these studies is whether genetic variance is natural or merely a laboratory artefact. Both lab strains used by Heisler (1984) were founded in 1970 and may have adapted differently to laboratory rearing conditions. Also, these lab strains were founded from single females collected from geographically distinct locations (MC-Mt. Carmel, Illinois; NB-Niobara, Nebraska). It is unclear whether these preference genes are polymorphic or fixed in the wild or whether they represent evolutionary change since the strains were founded. The same problems are encountered interpreting the results reported by Scott (1994), especially as Canton-S is an old lab strain (probably American in origin) whereas Tai-Y was founded over 10 years ago using a female from the Ivory Coast, Africa. These are general problems with *Drosophila* studies. Another example is the old study of eye

colour mutants (w white and w^a white apricot) by Tebb and Thoday (1956). They found that w/w homozygous females show stronger discrimination in favour of w^a/w^a over w/w males but that heterozygous w/w^a females show reversed preference for w/w males. What this tells us about natural genetic variation in female preference is unclear.

Quantitative genetic studies

More studies have shown the existence of quantitative genetic variation in mate preferences (Tab. 2b). 15 of the 17 cases have demonstrated significant genetic influences. The inclusion of examples in this part of the table is really an indication of ignorance about the genetic basis of female preference (e.g., linkage, number of genes) rather than knowledge of polygenic inheritance. Several of the examples from Table 2a might have been included here instead. For example in Heisler's (1984) study of *Drosophila*, the genetic analysis only provides a minimum estimate of *at least* two genetic elements, with only the most general information about linkage. Only 4 studies estimate the heritability of mating preference, so it is too early to draw conclusions about the extent of additive genetic variance of mating preference. But we can draw the general conclusion that mating preferences show significant additive genetic variances like other quantitative traits.

A common technique for demonstrating additive genetic variance is direct selection on mate preference. A good example is the selection experiment on the common field grasshopper *Chorthippus brunneus* (Charalambous et al., 1994). Adult grasshoppers were collected from a single population and their offspring tested for acoustic preferences. Females were given a choice of short and long syllable length calls and individuals with the strongest preference in both directions were selected for the next generation. There was marked divergence of female preference in the first generation offspring which declined in the subsequent two generations. The power of this experiment is limited because only one replicate line was created for each direction of selection. Drift can easily be important in experiments where few individuals are selected to form the next generation. A second problem with the experimental design was that the selection regime picked out females with a greater response to one of the two calls (ratio of responses) as well as those who were quicker responders. Responsiveness increased in each generation and this may have obscured true differences in preference between the lines. In spite of these difficulties the results suggest that there might be additive genetic variance in female acoustic preference in natural populations of the common field grasshopper but this remains to be confirmed.

A number of selection studies have been carried out on *Drosophila* (Cook, 1973; Crossley, 1974; Koepfer, 1987; Aspi, 1992). One advantage of using *Drosophila* is that genetic markers can be used. Crossley (1974) investigated the evolution of isolation between strains of *D. melanogaster* kept in sympatry. She selected for assortative mating between stocks carrying distinct phenotypic markers, ebony body colour and vestigial wings, both of which have marked effects on male

courtship. Each generation hybrid progeny were discarded. After more than 40 generations the frequency of hybrid matings was greatly reduced. Reproductive isolation was in part due to females showing much increased repulsion of heterogamic males. Two other studies have selected for increased female response to wingless males (Cook, 1973; Aspi, 1992) and again demonstrated the presence of additive genetic variance. A similar experiment selected for sexual isolation between wild caught *D. mojavensis* from Sonora and Baja in California (Koepfer, 1987). A rapid increase in isolation was found between Sonora females and Baja males (but not in the reciprocal direction). One of the main causes was increased mating preference amongst Sonora females for their own males. This demonstrates the presence in a natural population of additive genetic variance in mate preference.

Another interesting *Drosophila* study has been carried out on the *X* linked *per* locus (Greenacre et al., 1993). Mutations at the *per* locus alter the rhythmic component of male courtship song. Both wildtype and *per* mutant females prefer wildtype song (55 ms period) over artificial songs (40 ms and 80 ms) which suggests separate genetic control for song period and preference. However, females from an old mutant stock established in the early 1970s, with short song period (40 ms), showed no discrimination against mutant song compared to wildtype song. The continual exposure of this stock to mutant male song appears to have led to evolution in female mate preference in a relatively short time (about 20 years or 500 generations), indicative of the presence of genetic variance in preference. Similar evolution of female mate preferences has been reported in Japanese populations of the melon fly, *Dacus cucurbitae* (Hibino and Iwahashi, 1991). Flies on Okinawa island now discriminate against mass reared, sterile males that have been released there for many years. Ten years before they showed no discrimination. In contrast, females from Ishigaki island, where there has been no sterile male release, are equally likely to accept mass reared males as wild males. These examples chart evolutionary change under unusual circumstances. But they both show that female preference is a labile character that can respond to novel evolutionary pressures.

Another common technique for uncovering additive genetic variance is to look for correlated response in female preference due to selection on the male sexual trait. This has the advantage that male sexual traits are usually more easily and accurately measured. Six studies have revealed a genetic basis to female preference in this way including fruit flies (Ikeda and Maruo, 1982), pink bollworms (Collins and Cardé, 1989b), planthoppers (De Winter, 1992), stalk-eyed flies (Wilkinson and Reillo, 1994), sticklebacks (Bakker, 1993) and guppies (Houde, 1994). We treat these cases in detail in the following section.

In a similar way to selection experiments, Butlin (1993a) has used isofemale lines to detect genetic variation in female response to male substrate-transmitted vibrations in the brown planthopper, *Nilaparvata lugens*. A single gravid female was used to establish each line maintained by sib-mating. Female offspring were then tested for their response to a range of frequencies of synthetic male calls. There was no difference in the mean preference but large differences in the strength of female preference (width of acceptable male calls) between lines.

Finally a few studies have reported parent-offspring correlations in mating preferences. Male response to female pheromone in the pink bollworm moth, *Pectinophora gossypiella*, was estimated to have a positive heritability using parent-offspring correlation (Collins and Cardé, 1989a). This has been confirmed by selection experiments on preference (Collins and Cardé, 1990) and correlated change in preference caused by selection on the female pheromone blend (Collins and Cardé, 1989b; see below). Parent-offspring correlation studies in the cockroach, *Nauphoeta cinerea* (Moore, 1989), and the redbanded leafroller, *Argyrotaenia velutinana* (Roelofs et al., 1986), have also revealed evidence for genetic variance in female preferences. Again we treat these examples in more detail below as they provide evidence for genetic covariance.

Only a couple of studies that have seriously tried to measure genetic variance in female mating preference have found no evidence for it. Flour beetle, *Tribolium castaneum*, females significantly preferred male pheromone over blanks in choice tests, but in repeated choices females were highly variable in their responses, with no consistent patterns (Boake, 1989), Repeatability gives an estimate of the maximum heritability (Falconer, 1989) which in this case appears to be low. Measuring repeatability is an easy way to get an impression of genetic variance of choice in species where breeding under controlled laboratory conditions is impossible, and offers a good tool in field studies with marked individuals. Likewise Banbura (1992) did not find a significant repeatability of choice for male tail length between years in a Polish population of barn swallows, *Hirundo rustica*. However, there is a need in these studies to investigate other ways of measuring preference before it can be concluded that there is no significant heritability. Another study of barn swallows in Denmark has reported significant repeatability (Møller, 1994). When differences in the availability of potential mates were taken into account by taking the rank of the tail length of the chosen male relative to all males available in the breeding colony, female mating preference was repeatable (0.57 ± 0.11). However, consistency of choice need not be due to genetic differences: it could arise through environmental differences between females.

A second study reporting a lack of genetic variance is in red jungle fowl, *Gallus gallus*. In general females preferred males with long, bright red combs, red eyes and long tail feathers (Zuk et al., 1990). However, the mate choices of mothers and daughters were randomly distributed with respect to each of the male traits (Johnson et al., 1993). One reason for this inconsistency might be low additive genetic variance resulting from inbreeding. The population studied was from San Diego Zoo, and had been founded about 50 years ago with 30 birds from Southeast Asia. Again it is difficult to extrapolate much from this result without further studies of other populations.

Disruptive selection for morphological traits has been shown to result in partial sexual isolation between individuals with high and low trait values (e.g., pupal weight in *Tribolium casteneum* (Halliburton and Gall, 1981) and bristle number in *D. melanogaster* (Thoday and Gibson, 1970) but with no success in a follow up study (Spiess and Wilke, 1984)). This assortative mating might be due to evolutionary change in female mating behaviour but this has not been established, so we do

not include these as examples of genetic variance in mate preference. We also did not consider the extensive work on the evolution of sexual isolation in *Drosophila* through selection for assortative mating because it is unclear whether the male or female or both are involved (reviewed in Butlin, in press).

Genetic covariance between preference and preferred characters

The presence of genetic variance in mate preference raises the possibility of genetic covariance with the preferred sexual character as predicted by theory. Positive correlations between preferences and preferred signals between populations (Tab. 1) confirm that signallers and signal receivers have coevolved and complement similar findings between species (Butlin and Ritchie, 1989). But these correlations provide only suggestive evidence that significant genetic covariance is maintained within populations. In the absence of covariance, a number of mechanisms of sexual selection can not currently be operating, in particular runaway and the handicap mechanism. If studies showed a general absence of measurable genetic covariances within populations then we would have to radically revise a major intuition about sexual selection, that one of its main functions is selection of mates with high genetic quality.

In the last few years have there been a number of specific attempts to measure genetic covariance within populations. There are now 11 studies (Tab. 3). These go a long way to validating the theoretical prediction of genetic covariances caused by female mate choice. Almost all genetic correlations are positive but, unexpectedly, negative genetic correlations are also possible. No significant genetic covariance was found in a number of selection studies (Collins and Cardé, 1990; Charalambous et al., 1994; Breden and Hornaday, 1994) and there are some cautionary observations to draw about those studies with positive results. However, there are many ways to satisfy the null hypothesis of no relationship that are not demonstrations of the absence of genetic covariance. The most likely reason for failing to reject the null hypothesis is that the experimental design provides insufficient opportunity for preferential mating to maintain any genetic correlation. We now treat in detail the four most convincing recent studies.

Stalk-eyed flies: the longer the better

Southeast Asian stalk-eyed flies manifest a remarkable sexual dimorphism in eye span. Males and females have similar body sizes (males slightly larger) but males have far longer eye stalks than females relative to body size (Burkhardt and de la Motte, 1988). This has led to the seemingly absurd extreme, in a newly found species from Borneo, of males with 20 mm eye span far exceeding their body length, a mere 8 mm (Burkhardt et al., 1994). During the day flies forage alone on decaying plant material. In the evening they move to streams and form aggregations on root

hairs underneath banks where mating occurs at dawn and dusk (Burkhardt and de la Motte, 1988; Wilkinson, 1993).

Sexual selection for long eye span is caused by male-male competition and female choice. In *Cyrtodiopsis whitei*, Burkhardt and de la Motte (1988) used dead males to remove the effect of male-male competition. Dead males were mounted in natural postures on threads. When offered a choice between a male with medium eye span (8.5 mm) or long eye span (10.5 mm), females clearly preferred the male with the long eye span. Females also showed preference for supernormal males created by adding a piece of eye stalk (14 mm) but no control for the manipulation was carried out. In another experiment, population cages were set up with males and females from different allozyme marker strains of *C. whitei* allowing the assessment of paternity. Males with longer eye span sired relatively more offspring and the more so the greater the difference in eye span between the males (Burkhardt et al., 1994). In the related species *C. dalmanni*, females also demonstrate preference for males with long eye span (Wilkinson and Reillo, 1994). Simultaneous female choice experiments in the laboratory with two males that differed in relative eye span but not in body length (males created by artificial selection) showed clearly that naive females preferred the male with the longest eye span. This occurred irrespective of male-male competition; in one test males could interact freely, whereas in a second male-male competition was excluded by separating the two males by a clear partition with holes large enough for females but too small for males to move through.

A genetic analysis of sexual selection in *C. dalmanni* was carried out using two way selection for relative male eye span (Wilkinson, 1993). A large sample of flies was collected in Malaysia and maintained in the laboratory for 7 generations before selection experiments started. Flies were artificially selected for increased and decreased ratio of eye span to body length for 13 generations. Two selection lines in each direction and two unselected controls were maintained. Selection was highly successful in both directions. Responses in upward and downward directions were symmetrical. The estimated mean realised heritability for relative eye span in the first 10 generations of selection was 0.35 ± 0.06. Crosses between the lines after 13 generations indicated that the genes which influence relative eye span combine additively and do not exhibit sex linkage or maternal effects.

Wilkinson and Reillo (1994) also tested for correlated responses in female preference. After selection females from the short line preferred males with shorter eye span, the reverse of the normal preference. This appears to demonstrate a positive genetic correlation between the degree of expression of female mating preference and exaggerated male trait. Females from the long line preferred males with longer eye span but there was no difference between long line and control females. A number of explanations for this are possible. The most likely is that the mate choice test used was too insensitive to discriminate between long line and control females. Other possibilities are that female preference has already reached a selection limit in natural populations or that short and long lines differ because of drift.

Table 3. Genetic covariation of mating preference and preferred trait.

Organism	Preferred trait (male unless stated)	Reference
Insects		
cockroach *Nauphoeta cinerea*	olfactory cues related to dominance	Moore, 1989, 1990
common field grasshopper *Chorthippus brunneus*	call (mean syllable length)	Charalambous et al., 1994
fruitfly *D. mercatorum*	call (interpulse interval)	Ikeda and Maruo, 1982
planthopper *Ribautodelphax imitans*	female call (interpulse interval)	De Winter, 1992
pink bollworm *Pectinophora gossypiella*	a) female pheromone titre	Collins & Cardé, 1990 Collins et al., 1990
	b) female pheromone blend	Collins & Cardé, 1989b, 1990
redbanded leafroller *Argyrotaenia velutinana*	female pheromone blend	Roelofs et al., 1986
seaweed fly *Coelopa frigida*	body size associated with inversion karyotype	Gilburn et al., 1993 Gilburn & Day, 1994

h^2 preferred trait $\pm$ SE	$r_a \pm$ SE	Genetical method	Comment
high (*)	+ive (*)	father-daughter	daughters with dominant fathers prefer smell of dominant males and those with subordinate fathers show no discrimination
(*)	(NS)	CR (male trait) to two way selection for female preference	marked divergence between lines in first generation but not by third generation when correlated response checked
0.32 ± 0.04 (*) low, 0.14 ± 0.09 (*) high line	+ive (*) low, −ive (*) high line	CR (female preference) to two way selection for male trait	control and low line females prefer own males but high line females prefer to mate disassortatively
0.56 ± 0.05 (*) high, 0.78 ± 0.05 (*) low lines	+ive (*) mating test, (NS) choice test	CR (male preference) to two way selection for female trait	correlated change in male preference evident in assortative mating test but not in call playback experiment
0.71 ± 0.13 (*) (selection expt.), 0.41 ± 0.09 (*) (full sib analysis)	(NS)	CR (female trait) to two way selection for male preference and vice versa	selection on male preference caused no response in female pheromone, selection on pheromone titre caused no response in male preference; females allocated to males at random
0.50 ± 0.04 (*) high line, no response in low line, 0.34 ± 0.08 (*) (full sib analysis)	+ive (*) selection for blend, (NS) selection for preference	CR (male preference) to two way selection for female trait and vice versa	selection only successful for higher % ZE component of pheromone; high line showed a correlated response in male preference
0.41	+ive (*)	father-daughter	daughters produce a higher % ZE blend if their fathers respond positively to high % ZE blend pheromones
0.50 (*)	+ive (*) non tidal, −ive (*) tidal populations	correlation of preference with inversion karyotype	in non-tidal populations size and preference for size ordered $\alpha\alpha > \alpha\beta > \beta\beta$; in tidal populations, preference for size in the reverse order $\beta\beta > \alpha\beta > \alpha\alpha$

Table 3. (continued).

Organism	Preferred trait (male unless stated)	Reference
stalk-eyed fly *Cyrtodiopsis dalmanni*	relative eye span	Wilkinson & Reillo, 1994
Fishes		
guppy *Poecilia reticulata*	relative area of orange	Houde, 1992, 1994
guppy *Poecilia reticulata*	total coloration	Breden & Hornaday, 1994
three-spined stickleback *Gasterosteus aculeatus*	intensity of red breeding coloration	Bakker, 1993

Sticklebacks: the redder the better

The threespine stickleback, *Gasterosteus aculeatus*, is a small fish that breeds in fresh or brackish water (Bell and Foster, 1994). In spring, male sticklebacks develop conspicuous nuptial coloration consisting of an orange-red throat and fore belly and blue-green eyes. Males interact aggressively while establishing territories in shallow water and subsequently build a tunnel-shaped nest of plant materials. Males spawn with multiple females (up to 20), after which they care for the eggs and young.

Sticklebacks have been intensely studied during the past 60 years and there exists much evidence about the cues used in female choice. Recent experiments gave the first formal proof that the intensity of the male stickleback's red breeding coloration is the main cue for female choice (Milinski and Bakker, 1990). Ripe females were given a simultaneous choice of males that could not interact with each other. Under normal white light females preferred the redder male and discrimination increased with the difference in red intensity between the two males. Under green light females failed to discriminate between males and the females showed no preference no matter how large the difference in red intensity. The most obvious reason why females prefer redder males is that coloration reflects a male's ability to care for

h^2 preferred trait ± SE	$r_a \pm$ SE	Genetical method	Comment
0.35 ± 0.06 (*) (mean of selected lines; Wilkinson, 1993)	+ive (*) low, (NS) high lines	CR (female preference) to two way selection for male trait	reduced female preference in low lines, but no difference in high lines
0.55 (*) (median of selected lines)	+ive (*) and (NS)	CR (female preference) to two way selection for male trait	high line females show stronger preferences than low line females in 2 of 4 cases; divergence between lines decreased in 2nd and 3rd generations indicating loss of genetic covariance
0.18 (*) (median of selected lines)	(NS)	CR (female preference) to two way selection for male trait	effect of selection assessed after 5 generations was not significant
0.23 ± 0.27 (NS)	a) +ive (*) b) 0.75 ± 0.31 (*)	father-daughter brother-sister	redder fathers have choosier daughters; no effect of mother's choosiness on sons coloration

h^2 = heritability, r_a = genetic correlation, SE = standard error, NS = $p > 0.05$; * = $p < 0.05$, CR = correlated response to selection. Note standard error (SE) often an underestimate.

eggs and young. The intensity of red reflects energy intake when males are fed diets with the same carotenoid content, suggesting an energetic cost of being red (Frischknecht, 1993). In addition, the intensity of red is positively correlated with physical condition in different stickleback populations (Milinski and Bakker, 1990; Bakker and Mundwiler, 1994). Another possibility is that red coloration reflects male genetic qualities.

The genetics of female choice in sticklebacks was studied using a full-sib/half-sib breeding design (Bakker, 1993). Six extremely coloured males (3 intense red and 3 dull males) from a natural population were randomly crossed with a number of females from the same population (14 females in total). Paternal effects on offspring traits were excluded by removing clutches shortly after fertilisation and hatching them artificially under standard conditions. The intensity of red breeding coloration of male offspring resembled their fathers suggesting additive genetic variation of this male trait (heritability 0.23 ± 0.27 for red intensity). The mating preference of naive, gravid female offspring was tested in simultaneous choice tests. Repeated testing of preferences showed that females were consistent in their choice of redder males (repeatability 0.65 ± 0.14). A full-sib analysis gave a rough heritability estimate for preference of 0.43 ± 0.37.

A positive genetic correlation between female mating preference and preferred male trait was also demonstrated (Bakker, 1993). Father's intensity of red correlated positively with daughter's preference for red and son's intensity of red correlated positively with their sisters' preference for red across fathers. Thus redder fathers produced redder sons and daughters with stronger preference for red than did dull fathers. The estimated genetic correlation was 0.75 ± 0.31. Mothers had no detectable influence on their sons' red coloration or their daughters' preference for red. The maternal influence was stronger in crosses with dull fathers suggesting that dominance effects may have hidden the mothers' contribution. Maternal genetic effects would be easy to demonstrate if females from the extremes of the preference distribution were chosen as parents.

These experiments have been criticised because the population from which samples were taken is a recently founded population that may have been stocked with genetically distinct fish (Breden et al., 1994). The genetic covariance potentially could reflect this founding event rather than current selection. In fact, the last recorded introductions occurred in 1872, over 120 years ago. It seems unlikely that genetic correlations have been maintained over such an extended period. Another possibility is that there have been subsequent unrecorded introductions. The problem with this line of reasoning is that it leads nowhere without evidence of introductions and it is not clear whether even in principle it could explain the large genetic correlation observed (Pomiankowski and Sheridan, 1994b).

Guppies: an example of linkage disequilibrium?

Guppies (*Poecilia reticulata*) are in many respects comparable to sticklebacks. Guppies are small live-bearing fish, native to streams and rivers of Trinidad and adjacent parts of South America (Endler, 1980). They have a promiscuous mating system in which female mate choice among displaying males is a major cause of sexual selection. Guppies have a conspicuous colour dimorphism, males being much more conspicuously coloured than females. Colour patterns of male guppies vary within and between populations and there is a well documented trade-off between sexual and natural selection. This balance is reflected in a correlation between preferences and attractive male characters across populations (Tab. 1). The measurement of female preference in guppies is less straightforward than it is in sticklebacks, because sexual response of females is less obvious. The usual measure is time spent with a male in a simultaneous choice experiment (e.g., Breden and Stoner, 1987; Kodric-Brown, 1993) or the fraction of a male's courtship displays eliciting female sexual response (Houde 1987).

Reproductive success in guppies is related to multiple male criteria (Kodric-Brown, 1993). One of the few criteria for which female preference has been experimentally demonstrated is orange area (Long and Houde, 1989). Using two way selection for orange area and parent-offspring regression, Houde (1992) showed that orange area has Y-linked inheritance and a high heritability, the median estimate was 0.55 after 3–4 generations of selection. There was no obvious asymmetry between the upward and downward responses to selection.

In a separate experiment, Houde (1994) again selected on orange area but this time looked for evidence of a correlated response in female preference. Four replicate pairs of high and low selection were made. Every generation female preference was tested on a standard set of males. Selection was carried out for 3 generations. In each line male colour diverged significantly after one generation of selection. The effect of selection on female preference was mixed but points to a positive genetic correlation between the female preference and the male sexual trait. The overall effect after 3 generations was significantly stronger preference in the high lines compared to the low lines in 2 of the 4 replicates. The divergence in preference was greatest in the first generation and decreased with continued selection for the male trait. In the first two generations all 4 replicates showed significantly greater preference in the high lines. But by the third generation there was no distinct pattern. The overall pattern was inconsistent with divergence caused by drift.

The gradual decline in the correlated response to selection might well be explained by the social conditions under which the guppies were reared. Guppies used in the experiments were wild caught or offspring of wild-caught females. They were bred and maintained in small wading pools. Selection involved taking the 20 most extreme males and giving them 20 randomly selected females to mate with. Females were thus able to choose mates but under conditions that are probably more restrictive than in the wild. The experimental breeding conditions may not have been conducive to the maintenance of genetic variation in either trait, let alone a genetic covariance between them (Nichols and Butlin, 1987). One explanation for the weaker response to selection in later generations is that the covariance between preference and coloration broke down in the course of the experiment. Given that genes for male colour and female preference are unlinked (almost a necessity as colour is Y-linked), the genetic covariance will decrease by a half each generation without female choice to maintain it (Pomiankowski and Sheridan, 1994a). Another possibility is that inadvertant selection on preference occurred during the experiment and this counteracted the correlated increase in preference.

In a similar selection experiment, Breden and Hornaday (1994) selected male guppies for total coloration (proportion of body covered with pigmentation) for five generations. There were four replicate lines, two high and two low lines. The responses to selection were mixed: one of the high lines gave a good response (realised heritability 0.335), the other no response, whereas the two low lines gave moderate responses (realised heritabilities 0.145 and 0.211). These heritabilities are low compared to Houde's (1992) estimates. Fewer males, only 5, were selected each generation which would have increased the effect of drift.

After 5 generations of selection the correlated response in female preference was measured using a simultaneous choice test. In all replicates females exhibited similar preferences for the more colourful male. The results can be interpreted in two ways. The first possibility is that the lack of a measurable genetic correlation is a real reflection of the population examined. There are two facts that support this and suggest why the results are different from Houde's (1994) study. First, female choice for total coloration was not consistent when repeated (no data given). This low

repeatability suggests that genetic variation in female preference and thus any genetic correlation is small. This contrasts with the high repeatability of female choice for total coloration in another guppy population (Godin and Dugatkin, in press). Second, fish were sampled from the lower Aripo river, a population with high predation risk and inconspicuous males. Female preference in this population is not very pronounced (Breden and Stoner, 1987; Houde and Endler, 1990). Where preference is restricted by predation pressure and the physical characteristics of the environment theory predicts a low genetic correlation (Pomiankowski and Iwasa, 1993). On the contrary, Houde's (1994) genetic study used fish from the Paria river, a population with a low predation risk, pronounced male coloration and strong female preferences.

The second possibility is that there is a significant genetic correlation in the lower Aripo population but that the experimental design failed to detect it. Breden and Hornaday's (1994) breeding design provided no opportunity for female choice during the experiment. Each of the 5 selected males were allocated 4 randomly chosen females. In the absence of mate choice, the original linkage disequilibrium, if it existed, would not be maintained for long. This predicts that any correlated response would have occurred in the first few generations but could easily have been obscured by random changes induced by selection in later generations. Female preference was only assessed after 5 generations of selection, so it is impossible to know whether there was a correlated response early on. But this remains a possibility.

Seaweed flies: Fisher and good genes

A system that is totally different from the previous examples is found in seaweed fly, *Coelopa frigida*. It asks for different research methods and allows other conclusions to be drawn. Seaweed flies live on seaweed stranded on beaches of the North Atlantic and North Sea. They have a polygynous mating system. Females lay their eggs in seaweed where the larvae feed on bacteria that break down the seaweed. The stability of their food source varies greatly between populations (Gilburn and Day, 1994). In non-tidal populations seaweed is continuously available, whereas in tidal populations there are extended periods without food resulting in population crashes and genetic bottlenecks.

All populations of the seaweed fly are polymorphic for a large chromosomal inversion comprising about 10% of the genome and involving 200+ genes. No recombination occurs in this part of the genome in heterokaryotypes. The two alternative forms of the inversion, α and β, are associated with differences in development time, adult size, adult longevity and fertility (Butlin and Day, 1985). Large size is associated with $\alpha\alpha$, small size with $\beta\beta$ and $\alpha\beta$ heterokaryotypes intermediate. In effect the main determination of adult size is by a single segregation factor with two alleles (α and β). The α frequency is usually in the range of 0.3–0.4, and there is strong heterosis: the heterokaryotypes have a higher egg-to-adult viability (Butlin and Day, 1985).

Female preference was measured by observing female behaviour in single mating pairs of virgin flies in mating chambers until the male attempted to mount the female. Female behaviour during the first mount was scored as either acceptance or rejection if she curled her abdomen and prevented mating. The inversion karyotypes of flies were determined afterwards ruling out observation bias. Female preference was quantified in three tidal and three non-tidal populations. Linear regression of female acceptance rate on male size showed female mating preference for large male size in all populations (Gilburn et al., 1992, 1993; Gilburn and Day, 1994).

Genetic variation and covariation of female preference was studied by comparing preferences of the different inversion karyotypes. Preferences of the 3 karyotypes was different in tidal and non-tidal populations. In non-tidal populations, all karyotypes showed a preference for large males but preferences were strongest in $\alpha\alpha$ females, smallest in $\beta\beta$ females, and intermediate in $\alpha\beta$ females. In tidal populations the order of preferences was reversed: the strongest preference for large males was shown by $\beta\beta$ females, while $\alpha\alpha$ females preferred small males (though significantly so in only one population), and $\alpha\beta$ preferences were intermediate with an overall preference for large males (Gilburn and Day, 1994). The difference in choice behaviour between the two types of populations was thus greatest in $\alpha\alpha$ females and smallest in $\beta\beta$ females. Variation of female mating preference in seaweed flies is clearly associated with (but not necessarily located in) the inversion. Because α and β do not recombine, preferences can evolve independently on the α and β chromosomes, and seem to have done so in both tidal and non-tidal populations.

As male size and female preference are both in large part determined by inversion karyotype this means that there are strong genetic correlations between these two traits. Unfortunately, male karyotype has not been included in the analyses but in the interpretation of the results the authors make the assumption that male size is an indicator of inversion karyotype (but how reliable?). In tidal populations there is a tendency to disassortative mating with respect to size and karyotype. $\alpha\alpha$ females tend to mate with small $\beta\beta$ males and $\beta\beta$ females tend to mate with $\alpha\alpha$ males. Both these matings generate fitter $\alpha\beta$ progeny. This is a clear example of good genes sexual selection which, in this special genetic system, generates a negative genetic correlation between preference and preferred trait. In contrast, in non-tidal populations there is a general tendency to assortative mating with respect to both size and inversion karyotype. Non-tidal populations have a positive genetic correlation between preference and preferred trait. Gilburn and Day (1994) claim that the preference of $\alpha\alpha$ females in the non-tidal populations for large $\alpha\alpha$ males is evidence for Fisherian sexual selection because this choice generates the most attractive but not the fittest sons. This conclusion may be somewhat premature as long as net benefits of large body size remain to be determined. There are both negative and positive fitness effects of large body size: large flies take longer to develop, are worse competitors and have lower survival rates during the larval stage but have increased longevity ($\alpha\alpha$ flies live twice as long as $\beta\beta$ flies) and greater female fertility (Butlin et al., 1984; Butlin and Day, 1985, 1989).

Other studies

A number of other studies have reported evidence for and against positive genetic correlations (Tab. 3). In 3 studies the evidence for is good. In the cockroach, *Nauphoeta cinerea*, the strength of preference varies with paternal dominance. Female mate choice in *N. cinerea* is based on pheromone differences between males associated with male social status (Moore, 1988). In olfactometer tests females prefer dominant males. Females are consistent in their choice (Moore, 1989) and in natural populations dominance rank is heritable (Moore, 1990) suggesting that both traits are genetically variable. In order to study genetic covariance, dominant and subordinate males were mated to females chosen randomly and their female offspring tested for mate preferences. Daughters of dominant fathers preferred the odours of dominant males whereas daughters of subordinate fathers showed no preference (Moore, 1990).

Females use long-distance pheromones in the apple-feeding redbanded leafroller moth, *Argyrotaenia velutinana*, to attract males. Females produce a pheromone that consists of a 9 : 91 E/Z ratio of acetate isomers. The E/Z ratio is genetically variable, with estimated heritability of 0.41 from full sib analysis and 0.38 ± 0.07 from mother-daughter comparison (calculated from data in Roelofs et al., 1986, daughter means not weighted). Male attraction to pheromone was tested in a wind tunnel using 500 males from a recently established laboratory population. 80% of the males responded to a 8% E blend, 40% to a 15% E blend, and 10% to a 20% E blend. The few males that responded to the 20% blend also responded to the 8% E blend suggesting that these males had wider preference windows. Genetic correlation between female pheromone blend and male response was studied by comparing daughters of females that produce higher than average pheromone blends mated either with males that responded to the high blends (20% E) or with those that only responded to the low blends (8% E). The daughters from crosses with high responding males produced significantly greater amounts of the E isomer in their pheromones than the controls. In addition, 90% of the sons from the crosses between high females and high males responded to the 20% E blend, whereas in the laboratory population only 10% of males responded.

Not all studies are so encouraging. In the planthopper, *Ribautodelphax imitans*, both males and females communicate using substrate transmitted vibrations. The male initiates calling and when a female responds he may approach. De Winter (1992) selected for a property of the female call (interpulse interval) and looked for correlated changes in male preference. Selection was exerted in two directions with four replicates in each direction. Selection was highly successfull in both directions with realised heritabilities of 0.56 for the high lines and 0.78 for the low lines during the first 10 generations of selection. The correlated response in male preference was measured in two ways. Selected males were given a simultaneous choice of playback female calls from both selection lines. There was no significant difference in high and low line male responses compared to an unselected control. However, a second test revealed divergence between the selection lines. Two males from the same selection line were put with four females, two from each selection line. After some

time, females were checked for the presence of sperm in their spermathecae. There was positive assortative mating in both high and low line males. This hints at the possibility of genetic covariance. But the lack of differentiation between males in their response to synthetic calls makes it unclear why assortative mating occurs.

A second study showing weak evidence for genetic correlations carried out long-term selection on the interpulse interval of the male song in *Drosophila mercatorum* (Ikeda and Maruo, 1982). There was a good selection response in both low and high repetition rate lines, with realised heritabilities of 0.32 and 0.14 respectively after 11 generations. Correlated responses were measured by exposing females from low, high and control lines to combinations of males from two lines. Females from low and control lines showed preferences for their own males. But strangely high line females disfavoured their own males. This peculiar outcome seems to be associated with a general reluctance of high line females to mate with any males. However, the basis for these correlated changes were not investigated further and it is not entirely clear whether they are due to changes in female or male traits. Many other potentially confounding correlated changes were recorded (e.g., rate of development and body size).

Some weak evidence for genetic correlations have been found in an extensive study of the pink bollworm moth, *Pectinophora gossypiella*. Female moths produce a two-component pheromone consisting of a roughly 1 : 1 mixture of ZE and ZZ acetate isomers. Male preference for this pheromone was measured by quantifying the duration of wing fanning which is a short-range precopulatory behaviour (Collins and Cardé, 1989c). A number of genetic studies using different genetical methods have shown that there is appreciable additive genetic variation for both pheromone production and blend (Collins and Cardé, 1985, 1989b; Collins et al., 1990) and for duration of wing fanning (Collins and Cardé, 1989a, 1990).

Genetic correlation between the female sexual signal and male preference has been studied using the correlated response to selection on both male and female traits. In a line selected for female pheromone titre (one replicate) there was no correlated change in male preference (Collins et al., 1990). But selection for female pheromone blend caused some change in male response (Collins and Cardé, 1989b). Selection for decreased % ZE in the blend (one replicate) was not successful and selection was stopped after 5 generations. Selection for increased % ZE blend in the blend (one replicate) was successful. After 5 generations there was no evident correlated change in male preference but after 12 generations selected line males had significantly stronger preference for a high (65%) ZE blend. The response to low (25% and 44%) ZE blends was unchanged. With only one replicate selection line it is difficult to judge whether the correlated male response was due to selection or drift. There are additional problems in interpreting these results. Selection was carried out on a laboratory population that had been cultured for about 65 generations. This limits what can be said about genetic correlations in natural populations. In addition, during the selection procedure, females were assigned to males and there was little or no opportunity for mate choice. Thus, genetic correlations due to linkage disequilibrium between unlinked genes are unlikely to have been maintained through the experiment.

Collins and Cardé (1990) also successfully selected for increased male preference to a 65% ZE blend (one replicate). After 6 generations of selection, females were screened for changes in the titre and blend of the pheromone produced. No divergence occurred relative to an unselected control. But again there was little opportunity for mate choice during the experiment. Each generation about 20 selected males were put together with 50 randomly selected females in an oviposition cage. It is not at all obvious whether males in such a situation are able to use the long-distance female pheromone in their mate choice. Again, the effects of genetic drift cannot be ruled out with only one replicate.

Another study showing little evidence for genetic correlations selected on female preference in the common field grasshopper, *Chorthippus brunneus* (Charalambous et al., 1994; see above). Males sing a calling song that elicits stridulation of nearby females. Females that respond to the male's song are more likely to mate than unresponsive females (Butlin et al., 1985). Genetic covariance was measured in lines selected for female preference of either short or long mean syllable length (Charalambous et al., 1994). Correlated changes in male calling song were quantified in the third generation of selection. Though the selection procedure produced significant divergence in the first generation, by the third generation the difference in female preference between the high and low lines was no longer significant. It is not surprising then that neither was there a correlated change in mean male syllable length. Some other aspects of male song did show correlated changes but these are most probably due to drift. In the absence of replicate selection lines this cannot be verified.

Concluding remarks

The literature surveyed reveals that there is a surprisingly large body of evidence demonstrating genetic variation in mate preference (Tabs 1 and 2). Many studies looking for genetic variation have established its presence. Mate preference in this respect is like any other character. It is genetically variable and can potentially respond to selection. Most of the data reported has been collected in the last 5 years. Presumably the main reasons for the slow appearance of genetic studies are the difficulty of knowing how to accurately measure preferences and of working with animals that do not allow robust genetic analyses. These problems have caused a discrepancy between the animals favoured in behavioural studies of sexual selection (birds) and those used in genetical studies (insects), which suggests that the latter will become the favoured study organisms in the future. Precise estimates of the level of genetic variance in different species have not yet been made. Most studies have merely established that genetic variation is present. Another deficiency is that no genes for mate preference have been mapped beyond crude associations with regions of chromosomes. These obvious and important gaps in our knowledge wait to be filled.

More heritability estimates are available for the preferred male (or female) trait than for preferences. There are over 30 studies in which heritability has been

estimated for male sexual traits shown to be preferred by females (Pomiankowski, Møller and Bakker, unpublished data). The estimates are unexpectedly high (median > 0.50). The same holds for the standardized genetic variance which is often a more appropriate measure of evolutionary response (Houle, 1992).

It is clear that preferences and preferred sexual traits show genetic variance. We thus expect the existence of genetic correlations between mate preference and sexual traits as predicted by models of sexual selection. Our survey shows that a number of recent studies demonstrate the presence of genetic correlation in redbanded leafrollers, cockroaches, sticklebacks, stalk-eyed flies, guppies and seaweed flies (Roelofs et al., 1986; Moore, 1989; Bakker, 1993; Wilkinson and Reillo, 1994; Houde, 1994; Gilburn et al., 1993; Gilburn and Day, 1994 respectively) with some weaker evidence in fruitflies, pink bollworms and planthoppers (Ikeda and Maruo, 1982; Collins and Cardé, 1989b; De Winter, 1992 respectively). Genetic covariance is most likely caused by female mate choice. However, it has not been established whether it is due to linkage disequilibrium between unlinked genes or physical linkage of genes for preference and the sex trait. Physical linkage seems a most unlikely explanation in the case of the guppy because the male's colour genes show Y-linkage (Houde, 1994). But physical linkage must be important in seaweed flies where both preference and male attraction map mainly to a large inversion (Gilburn et al., 1993; Gilburn and Day, 1994). In the other cases, linkage disequilibrium and physical linkage have not been separated. There is an easy way to distinguish these possibilities: force random mating for a few generations. In the case of unlinked genes in linkage disequilibrium, recombination will reduce the genetic correlation each generation by 50% but with physical linkage the decay of genetic correlation will be much slower.

A number of studies failed to show genetic covariance (Collins and Cardé, 1990; Collins et al., 1990; Charalambous et al., 1994; Breden and Hornaday, 1994). These all used the same technique, looking for correlated responses in preference due to artificial selection on the preferred trait (or vice versa). In all cases, the experimental design provided little or no opportunity for mate choice during the selection procedure. The failure to find genetic covariance could thus just be the result of the loss of linkage disequilibrium due to recombination. When using artificial selection it is crucial to guarantee that females can still choose their mates. In the above mentioned selection studies mate choice was either excluded by forced random pairing in all generations (Charalambous et al., 1994), forced random pairing in the base population with limited opportunity of mate choice in later generations (Collins and Cardé, 1990; Collins et al., 1990), or limited mate choice during the whole selection experiment (Breden and Hornaday, 1994). Houde's (1994) study on guppies is illustrative in this respect. She followed the correlated response in female preference each generation. There was a gradual decline in the correlated response in each generation and by the third generation there was no longer any overall detectable correlated response in her 4 selection lines. In our view this strongly suggests that the covariance is due to linkage disequilibrium between unlinked genes which broke down during the experiment.

Another problem with selection studies is the lack of replicated lines. Drift by itself can cause lines to diverge which must make interpretation of correlated responses in single lines very tentative (e.g., Collins and Cardé, 1989b). The obvious solution is more replicates but this can be a very large undertaking. A further difficulty is that the standard error of heritability estimated from selection studies is often underestimated (Collins and Cardé, 1989b, 1990; Collins et al., 1990; De Winter, 1992). Due to autocorrelation of the generation means, the sampling variance of the regression of cumulative response on cumulative selection differential may easily be well below the correct value (Hill, 1971, 1972a, b). In selection studies the number of selected parents is small, so the variance of the population mean increases each generation due to genetic drift, and the generation means become correlated. In standard regression analysis the observations are assumed to have equal variance and be uncorrelated. After a few generations of selection most variance is contributed by drift. Hill (1972a, b) gives the correct approximations for calculating the sampling variance of heritability with different selection designs. The best estimate of the sampling variance of heritability is the direct estimate obtained from the variance between replicate selection lines. One or a few replicates will not be sufficient for this purpose.

When selection studies provided ample opportunity for mate choice during selection they were successful in showing genetic covariance after several generations of selection (De Winter, 1992; Wilkinson and Reillo, 1994). Our advice is that attempts to measure genetic covariance with artificial selection should provide plenty of opportunity for mate choice during the selection procedure and keep track of correlated responses in each generation. This advice is the opposite of Butlin (1993b), who argues for random pairing during artificial selection because mate choice may generate spurious genetic correlations. This seems a strange view as the point is to measure genetic correlations predicted to be generated by female mate choice. Female choice during the experiment prevents the decay of genetic correlations. The results of selection experiments support this and not Butlin's view. However, a less risky approach is to undertake genetic analyses for only one or two generations. All studies using this technique report the presence of genetic covariance (Roelofs et al., 1986; Moore, 1989; Bakker, 1993; Gilburn et al., 1993; Gilburn and Day, 1994).

Positive genetic covariance between mate preference and the preferred trait suggests that part of the reason for female mate choice and part of its current function is to select male for their genes. There are two obvious directions for future research involving genetic covariances. First, though genetic covariance *per se* is not a distinguishing feature between Fisherian and good genes sexual selection, by measuring offspring viability and mating success in the genetic analysis, the relative importance of these two modes of selection could be demonstrated (Iwasa et al., 1991). Second, it would be useful to have knowledge of the precise level of genetic variance and covariance in different populations to test theoretical predictions. Separate populations have only been studied in the seaweed fly and the Trinidadian guppy. Houde (1994) studied a guppy population from the Paria river and found genetic covariance, whereas Breden and Hornaday (1994) looked at a population

from the lower Aripo river and found no genetic covariance. This contrast may be an artefact of differences in experimental design (see above) but could be real (Pomiankowski and Sheridan, 1994a). Paria females have been recorded as having much stronger preferences than females found in the lower Aripo (Houde and Endler, 1990). The populations also differ in the number and type of visual predators (Houde and Endler, 1990). These differences and other ecological distinctions between the two populations might be responsible for divergence in the level of genetic covariance. Comparisons will also need to be made within species which have mate preferences for multiple sexual traits (Møller and Pomiankowski, 1993). Again this will help to comment on the importance of Fisherian and good genes sexual selection, a development we await with interest.

Acknowledgments

We thank Felix Breden, Roger Butlin, André Gilburn, Jean-Guy Godin, Anne Houde, Mike Ritchie, Gerry Wilkinson and an anonymous referee for access to unpublished manuscripts and comments on this work. TCMB is supported by the Swiss National Science Foundation and the Bernese "Hochschulstiftung". AP is supported by the Royal Society.

References

Alatalo, R. V., A. Carlson and A. Lundberg. 1988. The search cost in mate choice of the pied flycatcher. Anim. Behav. 36: 289–291.

Alexander, R. D. 1962. Evolutionary change in cricket acoustical communication. Evolution 16: 443–467.

Andersson, M. B. 1994. Sexual Selection. Princeton University Press, Princeton, New Jersey, U.S.A.

Arnold, S. A. 1983. Sexual selection: the interface of theory and empiricism, pp. 67–107. *In* P. Bateson (ed.), Mate Choice. Cambridge University Press, Cambridge, U.K.

Aspi, J. 1992. Female mate choice and mating system among boreal *Drosophila virilis* group species. Acta Univ. Ouluensis A 241.

Bakker, Th. C. M. 1993. Positive genetic correlation between female preference and preferred male ornament in sticklebacks. Nature 363: 255–257.

Bakker, Th. C. M. 1994. Genetic correlations and the control of behaviour, exemplified by aggressiveness in sticklebacks. Adv. Study Behav. 23: 135–171.

Bakker, Th. C. M. and B. Mundwiler. 1994. Female mate choice and male red coloration in a natural stickleback population. Behav. Ecol. 5: 74–80.

Banbura, J. 1992. Mate choice by females of the swallow *Hirundo rustica*: is it repeatable? J. Orn. 133: 125–132.

Barton, N. and M. Turelli. 1991. Natural and sexual selection on many loci. Genetics 127: 229–255.

Bell, M. A. and S. A. Foster (eds.). 1994. The Evolutionary Biology of the Threespine Stickleback. Oxford University Press, Oxford, U.K.

Boake, C. R. B. 1989. Repeatability: its role in evolutionary studies of mating behavior. Evol. Ecol. 3: 173–182.

Boake, C. R. B. 1991. Coevolution of senders and receivers of sexual signals: genetic coupling and genetic correlations. Trends Ecol. Evol. 6: 225–227.

Breden, F., H. C. Gerhardt and R. K. Butlin. 1994. Female choice and genetic correlations. Trends Ecol. Evol. 9: 343.

Breden, F. and K. Hornaday. 1994. A test of indirect models of selection in the Trinidad guppy. Heredity 73: 291–297.

Breden, F. and G. Stoner. 1987. Male predation risk determines female preferences in the Trinidad guppy. Nature 329: 831–833.

Burkhardt, D. and I. de la Motte. 1988. Big 'antlers' are favoured: female choice in stalk-eyed flies (Diptera, Insecta), field collected harems and laboratory experiments. J. Comp. Physiol. A 162: 649–652.

Burkhardt, D., I de la Motte and K. Lunau. 1994. Signalling fitness: larger males sire more offspring. Studies of the stalk-eyed fly *Cyrtodiopsis whitei* (Diopsidae, Diptera). J. Comp. Physiol. A 174: 61–64.

Burley, N. 1988. The differential-allocation hypothesis: an experimental test. Am. Nat. 132: 611–628.

Butlin, R. K. 1993a. The variability of mating signals and preferences in the brown planthopper, *Nilaparvata lugens* (Homoptera: Delphacidae). J. Insect Behav. 6: 125–140.

Butlin, R. K. 1993b. A comment on the evidence for a genetic correlation between the sexes in *Drosophila melanogaster*. Anim. Behav. 45: 403–404.

Butlin, R. K. in press. Genetic variation in mating signals and responses. *In* D. M. Lambert and H. G. Spencer (eds.), Speciation and the Recognition Concept: Theory and Application. John Hopkins University Press, Baltimore, U.S.A.

Butlin, R. K., P. M. Collins and T. H. Day. 1984. The effect of larval density on an inversion polymorphism in the seaweed fly, *Coelopa frigida*. Heredity 52: 415–423.

Butlin, R. K. and T. H. Day. 1985. Adult size, longevity and fecundity in the seaweed fly, *Coelopa frigida*. Heredity 54:107–110.

Butlin, R. K. and T. H. Day. 1989. Environmental correlates of inversion frequencies in natural populations of seaweed flies (*Coelopa frigida*). Heredity 62: 223–232.

Butlin, R. K., G. M. Hewitt and S. F. Webb. 1985. Sexual selection for intermediate optimum in *Chorthippus brunneus* (Orthoptera: Acrididae). Anim. Behav. 33: 1281–1292.

Butlin, R. K. and M. G. Ritchie. 1989. Genetic coupling in mate recognition systems: what is the evidence? Biol. J. Linn. Soc. 37: 237–246.

Capranica, R. R., L. S. Frishkopf and E. Nevo. 1973. Encoding of geographic dialects in the auditory system of the cricket frog. Science 182: 1272–1275.

Charalambous, M., R. K. Butlin and G. M. Hewitt. 1994. Genetic variation in male song and female song preference in the grasshopper *Chorthippus brunneus* (Orthoptera: Acrididae). Anim. Behav. 47; 399–411.

Collins, R. D. and R. T. Cardé. 1985. Variation in and heritability of aspects of pheromone production in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). Ann. Entomol. Soc. Am. 78: 229–234.

Collins, R. D. and R. T. Cardé. 1989a. Heritable variation in pheromone response of the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). J. Chem. Ecol. 15: 2647–2659.

Collins, R. D. and R. T. Cardé. 1989b. Selection for altered pheromone-component ratios in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). J. Insect Behav. 2: 609–621.

Collins, R. D. and R. T. Cardé. 1989c. Wing fanning as a measure of pheromone response in the male pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). J. Chem. Ecol. 15: 2635–2645.

Collins, R. D. and R. T. Cardé. 1990. Selection for increased pheromone response in the male pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). Behav. Genet. 20: 325–331.

Collins, R. D., S. L. Rosenblum and R. T. Cardé. 1990. Selection for increased pheromone titre in the pink bollworm moth, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae). Physiol. Entomol. 15: 141–147.

Cook, R. M. 1973. Courtship processing in *Drosophila melanogaster*. I. Selection for receptivity to wingless males. Anim. Behav. 21: 338–348.

Coopersmith, C. B. and S. Lenington. 1990. Preferences of female mice for males whose *t*-haplotype differs from their own. Anim. Behav. 40: 1179–1181.

Crossley, S. A. 1974. Changes in mating behavior produced by selection for ethological isolation between ebony and vestigial mutants of *Drosophila melanogaster*. Evolution 28: 631–647.

De Winter, A. J. 1992. The genetic basis and evolution of acoustic mate recognition signals in a *Ribautodelphax* planthopper (Homoptera, Delphacidae). 1. The female call. J. evol. Biol. 5: 249–265.

Dow, M. 1977. Selection for mating success of yellow mutant *Drosophila melanogaster*: biometrical genetic analysis. Heredity 38: 161–168.

Egid, K. and J. L. Brown. 1989. The major histocompatibility complex and female mating preferences in mice. Anim. Behav. 38: 548–550.

Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. Evolution 34: 76–91.

Engelhard, G., S. P. Foster and T. H. Day. 1989. Genetic differences in mating success and female choice in seaweed flies (*Coelopa frigida*). Heredity 62: 123–131.

Falconer, D. S. 1989. Introduction to Quantitative Genetics, 3rd ed. Longman, Harlow, U. K.

Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Clarendon Press, Oxford, U.K.

Frischknecht, M. 1993. The breeding colouration of male three-spined sticklebacks (*Gasterosteus aculeatus*) as an indicator of energy investment in vigour. Evol. Ecol. 7: 439–450.

Gilburn, A. S. and T. H. Day. 1994. Evolution of female choice in seaweed flies: Fisherian and good genes mechanisms operate in different populations. Proc. R. Soc. Lond. B 255: 159–165.

Gilburn, A. S., S. P. Foster and T. H. Day. 1992. Female mating preference for large size in *Coelopa frigida* (seaweed fly). Heredity 69: 209–216.

Gilburn, A. S., S. P. Foster and T. H. Day. 1993. Genetic correlation between a female mating preference and the preferred male character in seaweed flies (*Coelopa frigida*). Evolution 47: 1788–1795.

Godin, J.-G. J. and L. A. Dugatkin. in press. Variability and repeatability of female mating preference in the guppy. Anim. Behav.

Greenacre, M. L., M. G. Ritchie, B. C. Byrne and C. P. Kyriacou. 1993. Female song preference and the period gene in *Drosophila*. Behav. Genet. 23: 85–90.

Grula, J. W. and O. R. Taylor. 1980. The effect of X chromosome inheritance on mate-selection behavior in the sulfur butterflies *Colias eurytheme* and *C. philodice*. Evolution 34: 688–695.

Halliburton, R. and G. A. E. Gall. 1981. Disruptive selection and assortative mating in *Tribolium castaneum*. Evolution 35: 829–843.

Hammer, M. F. 1991. Molecular and chromosomal studies of the origin of *t* haplotypes in mice. Am. Nat. 137: 359–365.

Hansson, B. S., C. Löfstedt and W. L. Roelofs. 1987. Inheritance of olfactory response to sex pheromone components in *Ostrinia nubilalis*. Naturwissenschaften 74: 497–499.

Hansson, B. S., M. Tóth, C. Löfstedt, G. Szöcs, M. Subchev and J. Löfqvist. 1990. Pheromone variation among eastern European and a western Asian population of the turnip moth *Agrotis segetum*. J. Chem. Ecol. 16: 1611–1622.

Heisler, I. L. 1984. Inheritance of female mating propensities for yellow locus genotypes in *Drosophila melanogaster*. Genet. Res., Camb. 44: 133–149.

Heisler, I. L. 1994. Quantitative genetic models of the evolution of mating behavior, pp. 101–125. *In* C. R. B. Boake (ed.), Quantitative Genetic Studies of Behavioral Evolution. The University of Chicago Press, Chicago, U.S.A.

Henderson, N. D. 1989. Interpreting studies that compare high- and low-selected lines on new characters. Behav. Genet. 19: 473–502.

Hibino, Y. and O. Iwahashi. 1991. Appearance of wild females unreceptive to sterilized males on Okinawa Is. in the eradication program of the melon fly, *Dacus cucurbitae* Coquillett. Appl. Ent. Zool. 26: 265–270.

Hill, G. E. 1991. Plumage coloration is a sexually selected indicator of male quality. Nature 350: 337–339.

Hill, G. E. 1993. Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). Biol. J. Linn. Soc. 49: 63–86.

Hill, G. E. 1994. Geographic variation in male ornamentation and female mate preference in the house finch: a comparative test of models of sexual selection. Behav. Ecol. 5: 64–73.

Hill, W. G. 1971. Design and efficiency of selection experiments for estimating genetic parameters. Biometrics 27: 293–311.

Hill, W. G. 1972a. Estimation of realised heritabilities from selection experiments. I. Divergent selection. Biometrics 28: 747–765.

Hill, W. G. 1972b. Estimation of realised heritabilities from selection experiments. II. Selection in one direction. Biometrics 28: 767–780.

Houde, A. E. 1987. Mate choice based upon naturally occurring color-pattern variation in a guppy population. Evolution 41: 1–10.

Houde, A. E. 1992. Sex-linked heritability of a sexually selected character in a natural population of *Poecilia reticulata* (Pisces: Poeciliidae) (guppies). Heredity 69: 229–235.

Houde, A. E. 1994. Artificial selection on male colour patterns shifts mating preferences of female guppies. Proc. R. Soc. Lond. B. 256: 125–130.

Houde, A. E. and J. A. Endler. 1990. Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. Science 248: 1405–1408.

Houle, D. 1992. Comparing evolvability and variability of quantitative traits. Genetics 130: 195–204.

Ikeda, H. and O. Maruo. 1982. Directional selection for pulse repetition rate of the courtship sound and correlated responses occurring in several characters in *Drosophila mercatorum*. Jpn. J. Genet. 57: 241–258.

Iwasa, Y., A. Pomiankowski and S. Nee, 1991. The evolution of costly mate preferences. II. The 'handicap' principle. Evolution 45: 1431–1442.

Iwasa, Y. and A. Pomiankowski, in press. The evolution of mate preferences for multiple sexual ornaments. Evolution.

Joachim, D. and D. J. W. Curtsinger. 1990. Genotype and anesthetic determine mate choice in *Drosophila melanogaster*. Behav. Genet. 20: 73–79.

Johnson, K., R. Thornhill, J. D. Ligon and M. Zuk. 1993. The direction of mothers' and daughters' preferences and the heritability of male ornaments in red jungle fowl (*Gallus gallus*). Behav. Ecol. 4: 254–259.

Kearns, P. W. E., I. P. M. Tomlinson, C. J. Veltman and P. O'Donald. 1992. Non-random mating in *Adalia bipunctata* (the two-spot ladybird). II. Further tests for female mating preferences. Heredity 68: 385–389.

Klun, J. A., O. L. Chapman, K. C. Mattes, P. W. Wojtkowski, M. Beroza and P. E. Sonnet. 1973. Insect sex pheromones: minor amount of opposite geometrical isomer critical to attraction. Science 181: 661–663.

Kodric-Brown, A. 1993. Female choice of multiple male criteria in guppies: interacting effects of dominance, coloration and courtship. Behav. Ecol. Sociobiol 32: 415–420.

Koepfer, H. R. 1987. Selection for sexual isolation between geographic forms of *Drosophila mojavensis*. II. Effects of selection on mating preferences and propensity. Evolution 41: 1409–1413.

Lenington, S. 1991. The *t* complex: a story of genes, behavior, and populations. Adv. Study Behav. 20: 51–85.

Lenington, S. 1993. Mapping genes for female preference. XXIII IEC Conference Abstract 35.

Lenington, S., C. Coopersmith and J. Williams. 1992. Genetic basis of mating preferences in wild house mice. Am. Zool. 32: 40–47.

Lenington, S., K. Egid and J. Williams. 1988. Analysis of a genetic recognition system in wild house mice. Behav. Genet. 18: 549–564.

Löfstedt, C. 1993. Moth pheromone genetics and evolution. Phil. Trans. R. Soc. Lond. B 340: 167–177.

Löfstedt, C., B. S. Hansson, W. Roelofs and B. O. Bengtsson. 1989. No linkage between genes controlling female pheromone production and male pheromone response in the European corn borer, *Ostrinia nubilalis* Hübner (Lepidoptera, Pyralidae). Genetics 123: 553–556.

Löfstedt, C., J. Löfqvist, B. S. Lanne, J. N. C. van der Pers and B. S. Hansson. 1986. Pheromone dialects in European turnip moths *Agrotis segetum*. Oikos 46: 250–257.

Long, K. D. and A. E. Houde. 1989. Orange spots as a visual cue for female mate choice in the guppy (*Poecilia reticulata*). Ethology 82: 316–324.

Luyten, P. H. and N. R. Liley, 1991. Sexual selection and competitive mating success of male guppies (*Poecilia reticulata*) from four Trinidad populations. Behav. Ecol. Sociobiol. 28: 329–336.

Lyon, M. F. 1991. The genetic basis of transmission-ratio distortion and male sterility due to the *t* complex. Am. Nat. 137: 349–358.

Majerus, M. E. N., P. O'Donald and J. Weir. 1982. Female mating preference is genetic. Nature 300: 521–523.

Majerus, M. E. N., P. O'Donald, P. W. E. Kearns and H. Ireland. 1986. Genetics and evolution of female choice. Nature 300: 521–523.

Messina, F. J. 1994. Heritability and 'evolvability' of fitness components in *Callosobruchus maculatus*. Heredity 71: 623–629.

Milinski, M. and Th. C. M. Bakker. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature 344: 330–333.

Milinski, M. and Th. C. M. Bakker. 1992. Costs influence sequential mate choice in sticklebacks, *Gasterosteus aculeatus*. Proc. R. Soc. Lond. B 250: 229–233.

Millar, C. D. and D. M. Lambert. 1986. Laboratory-induced changes in the mate recognition system of *Drosophila pseudoobscura*. Behav. Genet. 16: 285–294.

Moore, A. J. 1988. Female preferences, male social status, and sexual selection in *Nauphoeta cinerea*. Anim. Behav. 36: 303–305.

Moore, A. J. 1989. Sexual selection in *Nauphoeta cinerea*: inherited mating preference? Behav. Genet. 19: 717–724.

Moore, A. J. 1990. The inheritance of social dominance, mating behaviour and attractiveness to mates in male *Nauphoeta cinerea*. Anim. Behav. 39: 388–397.

Møller, A. P. 1994. Repeatability of female choice in a monogamous swallow. Anim. Behav. 47: 643–648.

Møller, A. P. and A. Pomiankowski. 1993. Why have birds got multiple sexual ornaments? Behav. Ecol. Sociobiol. 32: 167–176.

Nevo, E. and R. R. Capranica. 1985. Evolutionary origin of ethological reproductive isolation in cricket frogs, *Acris*. Evol. Biol. 19: 147–214.

Nichols, R. A. and R. K. Butlin. 1989. Does runaway sexual selection work in finite populations? J. evol. Biol. 2: 299–313.

Norris, K. 1993. Heritable variation in a plumage indicator of viability in male great tits *Parus major*. Nature 362: 537–539.

O'Donald, P. and M. E. N. Majerus. 1992. Non-random mating in *Adalia bipunctata* (the two-spot ladybird). III. New evidence of genetic preference. Heredity 69: 521–526.

Paterson, H. E. H. 1985. The recognition concept of species, pp. 21–29. *In* E. S. Vrba (ed.), Species and Speciation. Transvaal Museum, Pretoria, South-Africa.

Petrie, M. and A. Williams. 1993. Peahens lay more eggs for peacocks with larger trains. Proc. R. Soc. Lond. B 251: 127–131.

Pomiankowski, A. 1988. The evolution of female mate preferences for male genetic quality. Oxford Surv. Evol. Biol. 5: 136–184.

Pomiankowski, A. and Y. Iwasa. 1993. Evolution of multiple sexual preferences by Fisher's runaway process of sexual selection. Proc. Roy. Soc. Lond. B 253: 173–181.

Pomiankowski, A. and L. Sheridan. 1994a. Linked sexiness and choosiness. Trends Ecol. Evol. 9: 242–244.

Pomiankowski, A. and L. Sheridan. 1994b. Female choice and genetic correlations. Reply. Trends Ecol. Evol. 9: 343.

Potts, W. K., C. J. Manning and E. K. Wakeland. 1991. Mating patterns in seminatural populations of mice influenced by MHC genotype. Nature 352: 619–620.

Potts, W. K. and E. K. Wakeland. 1993. Evolution of MHC genetic diversity: a tale of incest, pestilence and sexual preference. Trends Genet. 9: 408–412.

Reynolds, J. R. and M. R. Gross. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. Proc. R. Soc. Lond. B. 250: 57–62.

Ritchie, M. G. 1991. Female preference for 'song races' of *Ephippiger ephippiger* (Orthoptera: Tettigoniidae). Anim. Behav. 42: 518–520.

Ritchie, M. G. 1992. Behavioral coupling in tettigoniid hybrids (Orthoptera). Behav. Genet. 22: 369–379.

Roelofs, W. L., J.-W. Du, C. Linn, T. J. Glover and L. B. Bjostad. 1986. The potential for genetic manipulation of the redbanded leafroller moth sex pheromone blend, pp. 263–272. *In* M. D. Huettel (ed.), Evolutionary Genetics of Invertebrate Behavior-Progress and Prospects. Plenum Press, New York, U.S.A.

Roelofs, W., T. Glover, X.-H. Tang, I. Sreng, P. Robbins, C. Eckenrode, C. Löfstedt, B. S. Hansson and B. O. Bengtsson. 1987. Sex pheromone production and perception in European corn borer moths is determined by both autosomal and sex-linked genes. Proc. Natl. Acad. Sci. 84: 7585–7589.

Ryan, M. J., J. H. Fox, W. Wilczynski and A. S. Rand. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. Nature 343: 66–67.

Ryan, M. J., S. A. Perrill and W. Wilczynski. 1992. Auditory tuning and call frequency predict population-based mating preferences in the cricket frog, *Acris crepitans*. Am. Nat. 139: 1370–1383.

Ryan, M. J. and W. Wilczynski. 1988. Coevolution of sender and receiver: effect on local mate preference in cricket frogs. Science 240: 1786–1789.

Sappington, T and O. R. Taylor. 1990. Disruptive sexual selection in *Colias eurytheme* butterflies. Proc. Natl. Acad. Sci. 87: 6132–6135.

Scott, D. 1994. Genetic variation for female mate discrimination in *Drosophila melanogaster*. Evolution 48: 112–121.

Slagsvold, T., J. T. Lifjeld, G. Stenmark and T. Breiehagen. 1988. On the cost of searching for a mate in female pied flycatchers. Anim. Behav. 57: 37–48.

Spiess, E. B. and C. M. Wilke. 1984. Still another attempt to achieve assortative mating by disruptive selection in *Drosophila*. Evolution 38: 505–515.

Tebb, G. and J. M. Thoday. 1956. Reversal of mating preference by crossing strains of *Drosophila melanogaster*. Nature 177: 707.

Thoday, J. M. and J. B. Gibson. 1970. The probability of isolation by disruptive selection. Am. Nat. 104: 219–230.

van Noordwijk, A. J., J. H. van Balen and W. Scharloo. 1988. Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth. Genet. Res., Camb. 51: 149–162.

Vincent, A., I. Ahnesjö, A. Berglund and G. Rosenqvist. 1992. Pipefish and seahorses: are they all sex role reversed? Trends Ecol. Evol. 7: 237–241.

Wilczynski, W., A. C. Keddy-Hector and M. J. Ryan. 1992. Call patterns and basilar papilla tuning in cricket frogs. I. Differences among populations and between sexes. Brain Behav. Evol. 39: 229–237.

Wilkinson, G. S. 1993. Artificial sexual selection alters allometry in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). Genet. Res., Camb. 62: 213–222.

Wilkinson, G. S. and P. R. Reillo. 1994. Female choice response to artificial selection on an exaggerated male trait in a stalk-eyed fly. Proc. R. Soc. Lond. B 255: 1–6.

Williams, J. R. and S. Lenington. 1993. Factors modulating preferences of female house mice for males differing in *t*-complex genotype: role of *t*-complex genotype, genetic background, and estrous condition of females. Behav. Genet. 23: 51–58.

Yamazaki, K., G. K. Beauchamp, D. Kupniewski, J. Bard, L. Thomas and E. A. Boyse. 1988. Familial imprinting determines H-2 selective mating preferences. Science 240: 1331–1332.

Yamazaki, K., E. A. Boyse, V. Mike, H. T. Thaler, B. J. Mathieson, J. Abbott, J. Boyse and Z. A. Zayas. 1976. Control of mating preferences in mice by genes in the major histocompatibility complex. J. exp. Med. 144: 1324–1325.

Zouros, E. 1981. The chromosomal basis of sexual isolation in two sibling species of *Drosophila*: *D. arizonensis* and *D. mojavensis*. Genetics 97: 703–718.

Zuk, M., R. Thornhill, J. D. Ligon, K. Johnson, S. Austad, S. H. Ligon, N. W. Thornhill and C. Costin. 1990. The role of male ornaments and courtship behavior in female mate choice of red jungle fowl. Am. Nat. 136: 459–473.

Submitted 12 July 1994;
revised 13 October 1994;
accepted 3 November 1994.
Corresponding Editor: L. Hurst