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# GENETIC VARIATION IN FEMALE MATING PREFERENCE

by

THEO C. M. BAKKER

*(Universität Bern, Zoologisches Institut, Abteilung Verhaltensökologie, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland)*

## ABSTRACT

The existence of female mating preference has become well-established in an increasing number of animal species. Less well-investigated are the extent and causes of variation in female mating preferences. This paper reviews the evidence for the existence of intraspecific genetic variation in female mating preference, which is a crucial component of virtually all theoretical models of sexual selection. The influence of sexual imprinting on female mating preference is discussed.

KEY WORDS: sexual selection, female mating preference, behaviour-genetics, male secondary sexual characters, imprinting.

## SEXUAL SELECTION MODELS

More than a century ago DARWIN (1871) founded the theory of sexual selection which proposed female choice to explain the exaggerated sexual ornaments of the male sex in many species. He accepted female preference as given without attempting to explain its evolution. According to DARWIN's "aesthetic" view, females choose the males with the most attractive sexual ornaments.

FISHER (1930) extended DARWIN's aesthetic view by formulating a verbal model in which exaggerated male sexual ornaments evolve as a result of a coevolution of male ornament and female choice. It is assumed that there is no direct selection on female mating preference. Females with a preference for a particular male secondary sexual character produce sons which tend to possess genes for the preferred male trait and the female mating preference for that trait. These sons have a mating advantage because of their preferred trait and as a consequence the preference genes they carry are indirectly selected for. Female mating preference thus evolves as a correlated response to selection on the preferred male trait. This joint evolution is selfreinforcing and can result in a "runaway process" in which the preferred male ornament and female preference become exaggerated at everincreasing speed, even to a maladaptive extreme. Although FISHER (1930) had stated that "..., it is easy to see that the speed of develop-

ment will be proportional to the development already attained, which will therefore increase with time exponentially, or in geometric progression.'', it took some time before FISHER's ideas were translated into formal population genetic models. Haploid (KIRKPATRICK, 1982; SEGER, 1985) and diploid (O'DONALD, 1962, 1967; TOMLINSON & O'DONALD, 1989) few-locus models, as well as polygenic models (LANDE, 1981) have been constructed to study Fisherian sexual selection. The models assume a polygynous mating-system in which males show no parental care or mate discrimination. Thanks to these models known as ''Fisherian'', ''runaway'' or ''arbitrary trait'' models, this is the best understood type of sexual selection.

ZAHAVI's (1975) ''handicap principle'' is the main alternative to the Darwin-Fisher aesthetic view and its introduction caused a breakthrough of the interest in sexual selection by female choice, probably because many biologists found the claim of female mating preference for arbitrary (not connected to viability) male traits unsatisfactory. ZAHAVI argued that males with exaggerated sexual ornaments (''handicaps'') must be vigorous (*i.e.* have high viability) with respect to other characters (*i.e.* possess ''good genes''), otherwise they would not have been able to survive with the extra burden of the handicapping ornament. If viability is heritable, then females that prefer to mate with handicapped males wil tend to have offspring with higher than average viability. The ''Zahavi handicap'' mechanism has been much criticized (review, MAYNARD SMITH, 1985), partly because it would lead to a depletion of heritable variance in viability. Mate choice would then not result in fitter, more viable offspring and ultimately viability traits would be uncoupled from the handicap. Recent modelling showed that if additive genetic variance in viability is maintained (*e.g.* by recurrent deleterious mutation) the handicap principle does work (*e.g.* POMIANKOWSKI, 1988).

Among other ''viability-indicator'' models (also called ''good-genes'' or ''handicap'' models) the HAMILTON & ZUK (1982) host-parasite model offers an explanation for a sustained heritability of fitness. HAMILTON and ZUK interpret many of the male's exaggerated sexual ornaments as signals indicating parasite resistance (''revealing handicaps''; MAYNARD SMITH, 1985, 1987). They give females a chance to detect whether a potential mate is parasitized. Additive genetic variance in viability is maintained by the coevolution of a host population with its parasites, which in genetic models often leads to stable cycling (*e.g.* MAY & ANDERSON, 1983) and therefore to perpetual fluctuations in the direction of selection for parasite resistance. The HAMILTON & ZUK (1982) host-parasite model has attracted much attention both from theoreticians and empiricists (READ, 1988) and is a

serious candidate for the evolutionary explanation of exaggerated male ornaments and female preference for them.

This brief review has pointed out the main lines in sexual selection models. A further evaluation of sexual selection models can be found in *e.g.* KIRKPATRICK (1987a), POMIANKOWSKI (1988). The present paper aims to review empirical evidence for one of the premises of nearly all sexual selection models, namely intraspecific genetic variation in female mating preference.

## FEMALE MATING PREFERENCES

"With respect to sexual preference, experimental evidence of its existence in animals other than man is, and perhaps always will be, meagre." (FISHER, 1958, p. 150).

Experimental proofs of female mating preferences has accumulated only recently. The already classical example is ANDERSSON's experimental shortening and lengthening of the tail feathers of the long-tailed widow bird *Euplectes progne.* Females preferred to mate with males with the longest tails (ANDERSSON, 1982). Recently similar results were obtained with the male swallow's tail (MØLLER, 1988) and the male pheasant's spurs (VON SCHANTZ *et al.*, 1989).

In fish this kind of manipulation is less easily applicable without inducing behavioural changes, but transplantations of the sword of male swordtails (D. FRANCK, personal communication), surgically shortening of the tail of male guppies (BISCHOFF *et al.*, 1985), and the removal of egg-spots on the anal fin of a mouth-brooding cichlid fish by freeze-branding (HERT, 1986, 1989) have been carried out. Other methods have involved the use of dummies (BREDEN & STONER, 1987; ROWLAND, 1989) and artificial colouring with nailpolish or lipstick (SEMLER, 1971). All of these studies showed female preference for more exaggerated sexual ornaments. SEMLER showed that females from a population polymorphic for male breeding coloration preferred red males over non-red males. Female preference for artificially coloured non-red males over non-manipulated controls indicated that the females were responding to the red coloration alone. However, SEMLER's experimental design did not exclude effects either of red on male-male competition or of the paint itself. BAKKER & SEVENSTER (1983) applied SEMLER's recipe for a different purpose, but the paint came off during the experiments and the fish seemed to be adversely affected.

A more important question in sexual selection is whether females can detect small differences in secondary sexual characters rather than just discriminate between males with and without them. Recent

experiments on sticklebacks showed that they can (MILINSKI & BAKKER, 1990). When gravid female sticklebacks were given the choice between two territorial, nesting males which could not interact and which differed slightly in the intensity of red breeding coloration, they preferred the more red one. The influence of other factors besides colour was ruled out by partial correlation and an experiment in green light. Considering that male three-spined sticklebacks have very conspicuous breeding colorations among European freshwater fish species (DARWIN, 1871, himself mentioned the stickleback as an example) and the fact that they have been used as experimental animals in ethological studies for more than 55 years, makes it rather surprising that, apart from SEMLER's (1971) experiments and circumstantial evidence (WUNDER, 1934; TER PELKWIJK & TINBERGEN, 1937; CRONLY-DILLON & SHARMA, 1968; REISMAN, 1968; MCPHAIL, 1969; BAKKER, 1986; MCLENNAN *et al.*, 1988; MCLENNAN & MCPHAIL, 1989, 1990), it was only recently proven that the male's red breeding coloration is of importance in female choice. Thus far, emphasis had been placed upon the role of red coloration in aggressive encounters between stickleback males.

Female mating preference has been established for several species and new examples are continually being added to this list. The phenomenon should be borne in mind for instance when marking animals for ecological or ethological study (*e.g.* BURLEY *et al.*, 1982). Many aspects of female mating preference still have to be resolved (see BRADBURY & ANDERSSON, 1987). Little is known *e.g.* about whether females have absolute preferences or prefer a little or as much as possible extra exaggeration of sexual ornaments. Empirical interest has started to emerge for evolutionary aspects of female mating preference, *e.g.* inter-individual and inter-populational variation in the direction and extent of female mating preference and the role of genetics in this.

## GENETIC VARIATION IN FEMALE MATING PREFERNCE

"Perhaps the most crucial information needed at present concerns the genetic basis and magnitude of heritable variation for female mating preferences." (HEISLER *et al.*, 1987, p. 112).

This section reviews intraspecific behaviour-genetic studies on female mating preference. The limited number of studies that have been performed up to now, involving ladybirds, guppies, fruitflies and cockroaches, show that genetic varition in female mating preference does exist.

### *Ladybirds*

MAJERUS, O'DONALD and co-workers provided the first direct proof of genetic variation in female mating preference in a detailed study of the two-spot ladybird, *Adalia bipunctata* (MAJERUS *et al.*, 1982a; O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986; MAJERUS, 1986). The ladybird is polymorphic (both sexes) for the colour and pattern of the elytra and pronotum, with many distinct forms from all red to almost all black. These forms are determined by a multiple allelic series comprising at least 11 alleles at a single locus. In general, melanic forms (black with red spots) are dominant to non-melanic forms (red with black spots) (O'DONALD *et al.*, 1984). In England a common melanic form is *quadrimaculata* (black with four red spots); *typica* (red with two round black spots) is a common non-melanic form (*e.g.* MAJERUS *et al.*, 1982b; O'DONALD *et al.*, 1984).

All studies on preferential mating in the ladybird showed that *quadrimaculata* males mated more often than the *typica* males. This occurred in long-term experiments with large groups, shorter experiments with small groups, and in a wild population (phenotypes of mating and non-mating ladybirds in samples were recorded) (*e.g.* MAJERUS *et al.*, 1982a, b; O'DONALD *et al.*, 1984; O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986).

The frequency of melanics in a natural population (Keele, U.K.) was about 30% and there was an excess of melanics amongst mating pairs under the assumption of random mating. Population cage experiments showed that the mating advantage of *quadrimaculata* males was strongly frequency dependent (MAJERUS *et al.*, 1982b). Female mating preference necessarily gives rise to frequency-dependent selective advantage. Choosy females have fewer preferred males to select from when they are infrequent and therefore rare preferred males mate more often: the "rare male effect" which has frequently been observed *e.g.* for certain eye colour mutants in *Drosophila* (*e.g.* SPIESS & EHRMAN, 1978) and for body colour in the guppy (FARR, 1977). The rare male effect has often been questioned, and in some cases rightly so (see PARTRIDGE, 1989), because many biologists felt uncomfortable with the arbitrariness of the preferred male traits and argued that preferred traits will, in some way, be connected with viability. The Fisherian runaway sexual selection models show quite neatly that this is not necessary; runaway selection may lead to nonadaptive female choice (*e.g.* LANDE, 1981; KIRKPATRICK, 1982).

Male competition as an explanation for the mating advantage of *quadrimaculata* males was experimentally ruled out (see below). Actually, displacement of copulating males by males of the other

phenotype was not observed, neither in the laboratory nor in the field. The mechanism of sexual selection appeared to be female choice. Females were frequently seen to reject males and did so less often with *quadrimaculata* males than with *typica* ones (MAJERUS *et al.*, 1982b). A model was developed to provide an evolutionary explanation of the polymorphism of the two-spot ladybird (O'DONALD *et al.*, 1984; O'DONALD & MAJERUS, 1984). The observed stable polymorphism of melanic and non-melanic phenotypes was shown to be completely consistent with predictions of a combined model of natural selection (melanics suffer a disadvantage which is less in smoke polluted areas), sexual selection and assortative mating. Genetic variation was not included: the non-assortative preferences were expressed by all females regardless of their phenotype.

Genetic variation of female mating preference was shown in selection experiments. Selections for increased preference for *quadrimaculata* males (MAJERUS *et al.*, 1982a; O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986), for decreased preference (O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986) and unselected controls were made. In the high lines every generation was made up by the progeny of females that had mated with *quadrimaculata* males, in the low lines by progeny of females that had mated with *typica*, and in the control line by progeny of all mated females. Female mating preference could be substantially increased or reduced to the level of no preference in successive generations of the respective lines by artificial selection. No preferential mating with *typica* males evolved in the low lines. Apparently, a genetic preference only existed for melanics (fig. 1).

The possibility that male competitiveness (those melanic males that were the most active and quickest to mate might have been selected) had also been selected for at the same time as female mating preference, was tested in population cages using 3 different populations; one with high selection line males and unselected females, one with unselected males and females from the high selection line, and a third with unselected males and females (MAJERUS *et al.*, 1982a). If selection for increased mating preference for melanics had also made melanic males better competitors, then we would expect that high line melanic males would do better than unselected ones with females from the control line. Only with selected females was the level of female mating preference for melanic males characteristic of the high line. Selected males with unselected females attained the level characteristic of the unselected stock. Hence the selection experiments present a rigorous proof of the existence of genetic variation in female mating preference of ladybird beetles.

Many models have shown the feasibility of Fisherian sexual selec-

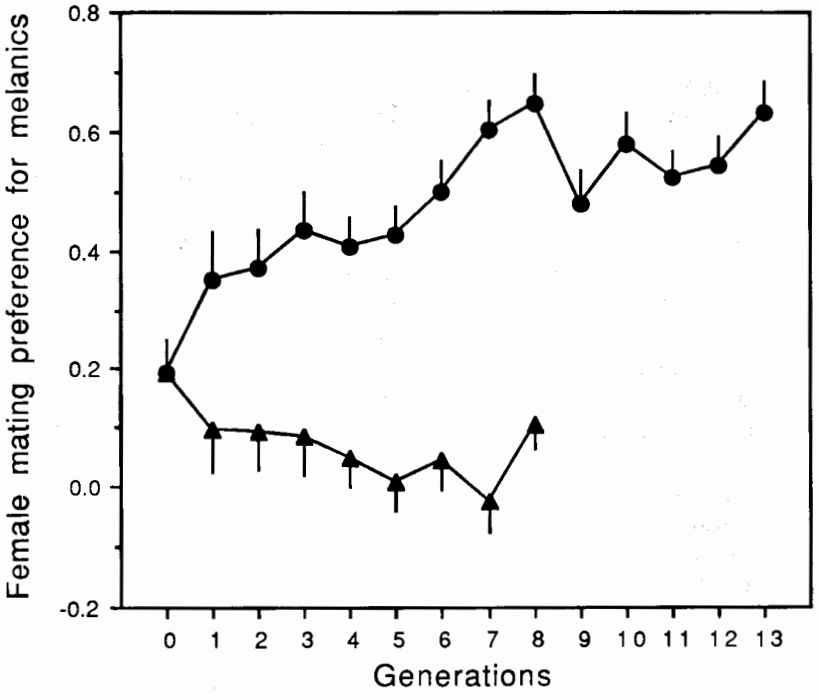


Fig. 1. Responses to selection for (circles + SD) and against (triangles-SD) female mating preference for melanic male ladybirds. After O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986.

tion. Nonetheless the models differ in some important respects (BORGIA, 1987; HEISLER *et al.*, 1987). For instance, the few-locus models, which only permit fixation of alternative alleles, cannot generate the coevolutionary escalation in secondary sexual traits and female mating preference (ARNOLD, 1985) that was described by FISHER (1930). Further, in the few-locus models the rate and ultimate outcome of the sexual selection process is critically dependent on the dominance relations of the preferred alleles.

The ladybird studies indicated that one or a small number of genes controls the variation of female mating preference (O'DONALD & MAJERUS, 1985; MAJERUS *et al.*, 1986). BULMER's model (in O'DONALD & MAJERUS, 1985), which treats the expression of preference as an all-or-nothing variable, gave reasonable estimates of heritability (high line: mean heritability = 0.38; low line: mean heritability = 0.08). The genetic basis of variation in female mating preference was tested with

isofemale lines (MAJERUS *et al.*, 1986). Randomly selected pairs from the tenth generation of the high selection line were used and the progeny of each mated pair was reared separately. Four distinct groups of lines could be distinguished: female progeny of some lines mated almost exclusively with melanics, while those of others mated at random or showed intermediate levels of preference. Similar results were found when unselected males, or males from other lines, were used instead of males from the same line as the females, showing again that female mating preference was responsible for the observed pattern. The quadrimodal distribution in preferences of isofemale lines is consistent with the hypothesis that female mating preference for melanic males is controlled by a single dominant gene.

Certainly, more behaviour-genetic studies on female mating preference are necessary, especially with respect to quantitative, sex-limited sexual ornaments of males. After all, the non-sex-limited polymorphism of elytra colour in ladybirds is not the character we have in mind when speaking of exaggerated sexual ornaments in males. Moreover, ladybirds with bright patterns are aposematic and unpalatable to many predators. Further, melanic ladybirds may be favoured in low light conditions because of their more efficient absorption of solar radiation. This may explain why melanism in the two-spot ladybird is associated with industrialization (*e.g.* BRAKEFIELD & WILLMER, 1985; BRAKEFIELD, 1987). It may be then not surprising to find that the preference gene for melanics is apparently absent or at very low frequency in some other populations of two-spot ladybirds (BRAKEFIELD, 1984).

### *Guppies*

The guppy, *Poecilia reticulata* has been an intensively studied fish species in sexual selection. Male guppies have conspicuous colour patterns, probably contribute only genes to the next generation (although some nutrients may be transferred with the spermatophore; J. A. ENDLER, personal communication), and among guppy populations there is great variation in colour patterns and behaviour. Guppies from the headwaters of streams are generally brighter coloured than those from downstream populations. In the latter populations conspicuous males are selectively preyed upon by large predatory fish, whereas these are absent upstream. In those populations bright, conspicuous males have evolved by female choice (ENDLER, 1978, 1980, 1983; BREDEN & STONER, 1987; STONER & BREDEN, 1988; HOUDE, 1988a; HOUDE & ENDLER, 1990).

HOUDE (1988a) compared female mating preference of two guppy populations in which the males differed in the extent and intensity of the orange pigment in their colour patterns. Males from the Paria river in Trinidad possess bright orange spots which cover a nearly twice as large body area than the smaller, paler orange or yellow spots of males from the Aripo river. The main predator of Paria males is a prawn, *Macrobachium*, which cannot see orange, while Aripo males are subjected to a greater predation pressure by several fish species which can see orange (ENDLER, 1978, 1983). In a previous study on the Paria population, HOUDE (1987) showed that the more extensive the male's orange colour pattern, the greater was the sexual responsiveness of females to male courtship and the sooner they copulated (see also ENDLER, 1983; KODRIC-BROWN, 1985). Choice experiments under various kinds of coloured light suggested that, besides the relative area of orange, general conspicuousness might also be a cue for female choice in guppies (LONG & HOUDE, 1989).

In the behaviour-genetic study on female mating preference, HOUDE (1988a) used fourth- and fifth-generation descendants of wild-caught stocks from the Paria and Aripo rivers. They had been held in the laboratory under identical conditions. Differences between the populations (*e.g.* in colour patterns and behaviour) were therefore likely to be genetically based. The sexual responsiveness of females, which had seen no sexually mature males before, to male courtship was quantified in mixed groups of which the members of one sex all belonged to the same population. Male attractiveness measured in this way was significantly correlated with mating success.

Paria females discriminated strongly between Paria males, whereas Aripo males did so only weakly. Paria females preferred males with high orangeness values and were less responsive to males lacking in orange, while such preference was absent in Aripo females (fig. 2). HOUDE & ENDLER (1990) recently extended these experiments and showed that the degree of female preference based on orange is positively correlated with the population average orange area.

Two further issues of general interest have been raised by the guppy studies. Similar phenomena have been found to occur in three-spined sticklebacks, *Gasterosteus aculeatus*, and probably also occur in other species. Colour cues on which female choice in guppies and sticklebacks is primarily based consists of colour pigments which reflect long wavelengths. The pigments are composed of carotenoids (*e.g.* BRUSH & REISMAN, 1965; KODRIC-BROWN, 1989) which are widely used for coloration in animals. A prerequisite for the evolution of these secondary sexual colour cues by female choice, irrespective whether female choice is adaptive or not, is that males cannot bluff with respect

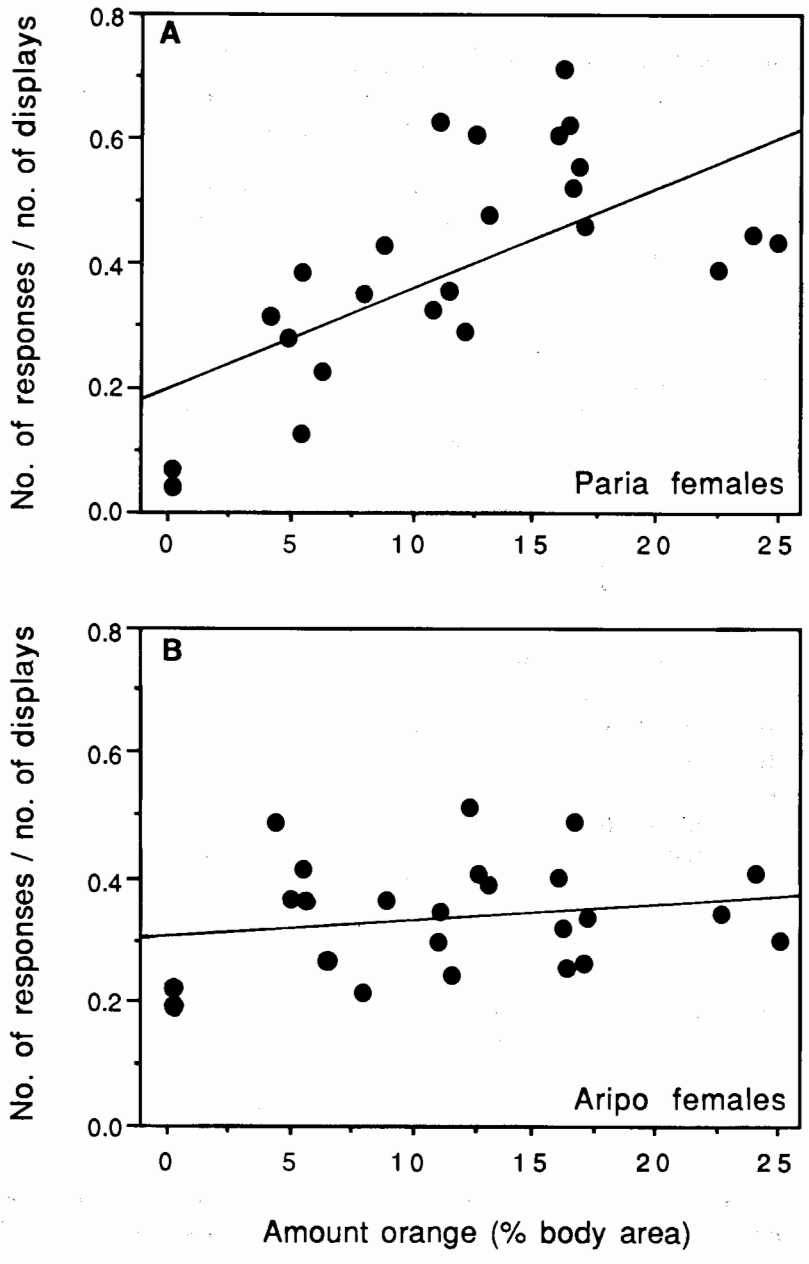


Fig. 2. The effect of differences in relative area of orange on female mating preference for Paria males of (a) Paria females ($y = 0.53x + 0.20$, $r^2 = 0.43$, $p < 0.001$) and (b) Aripo females ($y = 0.08x + 0.31$, $r^2 = 0.04$, $p > 0.25$). After HOUDE, 1988a.

to these colours. This means that in one way or the other it should be costly to build up and maintain such coloration. Several factors contribute to these costs. The most obvious one is the cost of predation. Males with exaggerated secondary sexual characters are also conspicuous to predators. In guppies the expression of male's colour patterns is clearly related to the predation pressure by piscivorous fish (ENDLER, 1978, 1980); in low-predation populations males have larger and more numerous spots (inclusive of orange spots) than males in high-predation populations. Further, the size and number of spots increases in populations where predation has been reduced or eliminated experimentally (ENDLER, 1980). The red breeding coloration of male sticklebacks makes them more vulnerable to predation as has been experimentally shown to be the case for red males from polymorphic populations over males lacking red (MOODIE, 1972). However, there is a lack of data on the predation-risk of male sticklebacks with less extreme differences in their red breeding coloration.

A second set of costs might be generated by the inability of animals to synthesize carotenoids *de novo*. The biosynthesis of carotenoids is known to be limited to plants and some microorganisms and animals must obtain carotenoids from their diet. Different prey items can vary greatly in their carotenoid content and high quality food might be limited. Intense breeding coloration might therefore reflect great foraging abilities and nutritional status (ENDLER, 1980, 1983; REIMCHEN, 1989). Once the carotenoids are ingested, they have to be transformed into the appropriate colour pigments and transported to the appropriate sites which may incur chemical costs. The development of secondary sexual characters is in many species dependent on male gonadal hormones (*e.g.* BAKKER, 1986). This dependency on androgens might at the same time set upper limits to the expression of the male's sexual ornaments, because high androgen levels might reduce survivorship (MARLER & MOORE, 1988) and, interestingly, they might increase susceptibility to parasites (*e.g.* MOLAN *et al.*, 1984; NAKANISHI *et al.*, 1989).

In sticklebacks, REIMCHEN (1989) showed for populations in eastern Canada that the greatest expression of red breeding coloration occurred in habitats with the highest water clarity, while loss of red breeding coloration was generally found in heavily stained waters. This might indicate that the costly red breeding coloration regresses when the positive selection pressure of sexual selection becomes weaker. A more direct proof of the costs of the male's red breeding coloration in sticklebacks was recently offered by MILINSKI & BAKKER (1990) in showing a significant positive correlation between the expression of

the red breeding coloration and physical condition of the males. An experimental reduction in condition by weakly parasitizing reproductive males with white-spot disease (*Ichthyophthirius multifiliis*) caused a significant decrease in the intensity of their red breeding coloration in comparison with unparasitized males (MILINSKI & BAKKER, 1990). This shows that the intensity of the red breeding coloration of male sticklebacks is a truly revealing handicap (MAYNARD SMITH, 1985, 1987).

In contrast with the proposed costs of possessing bright carotenoid breeding coloration, there might be benefits, in addition to those resulting from intra- (BAKKER & SEVENSTER, 1983; BAKKER, 1986) and intersexual selection, associated with having a high carotenoid content. The importance of some carotenoids as precursors of vitamin A (BAUERNFEIND *et al.*, 1971), which is involved in light perception in the eye is well known. Numerous additional beneficial metabolic and nutritional functions have been suggested (summarized *e.g.* in SEGNER *et al.*, 1989). Although up to now most of them are tenuous, they suggest that carotenoid breeding coloration might not only be considered as a revealing handicap, but also as a male trait that itself contributes to viability (MAYNARD SMITH, 1985, 1987). During egg formation carotenoids are mobilised from the muscle and the liver, laid down in the growing ovary, and later found in the mature eggs. It is generally accepted that carotenoids are not deposited fortuitously in the eggs of fishes and that they must serve some metabolic or other purpose in egg development (reviewed by CRAIK, 1985). Initially the yolk carotenoid serves simply as an external pigment and is deposited in the chromatophores of the embryonic skin. Additionally, there is growing evidence that carotenoids may perform some undefined function in the respiration of the egg or juvenile when oxygen levels are low. Large variation in the carotenoid content of eggs exists at the intrapopulation level. For example, laboratory-bred and -maintained female sticklebacks produce egg clutches which may considerably vary in colour, ranging from almost colourless (very pale yellow) to orange (WOOTTON, 1976; BAKKER, unpublished data). Taking this variation and the possible functions of carotenoids in eggs into account, it is tempting to suggest that by preferring intense red males, stickleback females not only produce "sexy sons" but "dowry-daughters" as well and both contribute to an increased production of grandchildren.

A second discussion point arising from the guppy studies is the finding that female behaviour was affected by the male colour pattern rather than by correlated differences in sexual behaviour (HOUDE, 1987; LONG & HOUDE, 1989). No relationship was found between orange area and display rate within populations. This finding is

important for the interpretation of the behaviour-genetic study of HOUDE (1988a), since predation risk affects both the male's colour pattern and his courtship behaviour quantitatively and qualitatively (FARR, 1975; LUYTEN & LILEY, 1985; ENDLER, 1987; MAGURRAN & SEGHERS, 1989) in the same direction of reduced conspicuousness. The significance of the male's courtship intensity on female choice needs further study, because several other guppy studies did show an effect on female choice (FARR, 1980; BISCHOFF *et al.*, 1985; KENNEDY *et al.*, 1987). However, these studies did not control for colour differences between the males and/or their experiments were not conducted under comparable light intensities. Independent of the presence of predators, male guppies courted and used visually conspicuous behavioural elements less often under high light levels (ENDLER, 1987). When female guppies were given a choice between a bright but nonresponsive male and a drab but responsive male from different populations, they chose the brighter one, indicating that brightness was more important than responsiveness (STONER & BREDEN, 1988).

Whatever the reason may be for the above controversy in the guppy literature, the impact of male behaviour on female choice in HOUDE's studies are in agreement with findings in sticklebacks (MILINSKI & BAKKER, 1990). In sticklebacks, female choice was primarily based on red breeding coloration. Colour intensity but not courtship intensity was correlated with physical condition. This raises questions as to the function of courtship displays. It is likely that a minimum display rate is needed for mate and species recognition and to attract the attention of ripe females from a distance. Maybe it is ethologically too provocative to assume that the courtship display evolved for advertising optimally the male's red breeding coloration. A phylogenetic analysis of the Gasterosteidae using behavioural characters suggested that initially colour was not necessary in courtship but that it later became intimately involved in male-female interactions (MCLENNAN *et al.*, 1988). It is therefore more plausible to assume that in the evolution of the male's red breeding coloration of the three-spined stickleback the red colour became concentrated at sites in the skin where an optimal balance was met between visibility towards predators and effectiveness during courtship.

Another guppy study that claimed to have shown a genetic populational difference in the degree of female preference is that of BREDEN & STONER (1987). Single female offspring of wild-caught parents were given a choice between a drab and a bright male model and her position relative to the male models was recorded. Females of low-predation populations preferred the bright model, while those of high-predation populations on average preferred the drab model.

The BREDEN & STONER (1987) study (see also STONER & BREDEN, 1988) thus indicated that guppy populations subjected to different predation-risks were genetically differentiated for female mating preference. Both the Fisherian and viability indicator models of sexual selection predict this. According to the Fisherian models a response of male colour pattern to a change in natural selection (*e.g.* predation pressure) should lead to a correlated response in female mating preference. According to the viability indicator models female mating preference should diverge if the relationship between male colour pattern and viability of offspring differs between populations.

The BREDEN & STONER (1987) paper, however, has been seriously criticized (ENDLER, 1988; HOUDE, 1988b) for the following main reason. The painted models were as much as four times larger than real males and, in addition, BREDEN & STONER placed an aerator only near the brighter model. As the size of the models was similar to that of several potential fish predators of guppies, both these flaws in the experimental design might well have caused a distinct asymmetry in the fright response between females of the high- and low-predation population. This alone renders their conclusions on female mating preferences questionable.

### *Fruitflies*

This section deals with three different studies on *Drosophila melanogaster*. These studies are well spaced chronologically and this shows that genetic variation in female fruitflies' mating preference has been largely neglected, though mating behaviour in *Drosophila* has been the focus of many studies. These were, however, concentrated for a long time on reproductive isolation and speciation and in this respect there exist a small body of literature on the genetic basis of assortative mating.

Recently JOACHIM & CURTSINGER (1990) warned that conclusions regarding mating preference are sensitive to the anesthetic used prior to testing; etherization of *D. melanogaster* at emergence had lasting effects on mating behaviour. The major determinant of mating choice in their experiments was due to an interaction effect between genotypes and mode of anesthesia.

An early experiment by TEBB & THODAY (1956) suggested the existence of genetic variation in female mating preference. They tested female mating preference for two eye-colour mutants of females homozygous for one or the other allele and the heterozygous females. Single females were tested for their preference by putting them in a food tube with one male of each kind, and scoring the phenotypes of

their offspring to assess fatherhood. The heterozygote females preferred to mate with a different male genotype than did the two homozygotes. The experiment showed that differences of preference can be associated with differences of genotype.

Another *Drosophila* study was set up to show that changes in mating behaviour induced by artificial selection for assortative mating contribute to increased sexual isolation (CROSSLEY, 1974). As she combined the selection experiments, unlike several others, with a behavioural analysis, this study also yielded useful data on the genetics of female mating preference. The selection experiments were carried out with two mutant strains of *Drosophila melanogaster:* an *ebony* (*e:* dark body coloration) and a *vestigial* (*vg:* reduced wings) strain. Each generation was made up from the progeny of those females that had mated with their own kind in a large mixed population. The selection experiment for assortative mating was run for 40 successive generations. A control line was maintained in the same way as the selected lines but without exerting a selection against hybrids.

At the start of the selection experiments mating was non-random, that is, *e* females mated more often with *e* males than with *vg* males. *vg* females mated non-preferentially with both males. With the progress of selection a significant increase was obtained in both kinds of assortative matings, and a concomittant decrease in the percentage of hybrid matings. In order to determine whether these changes in mating behaviour were due to changed male behaviour, changed female behaviour or to both, in later generations of selection mating behaviour of single pairs of selected flies was quantified and compared with that of pairs of outcrossed mutant stocks.

First, selection had changed male behaviour. Male courtship became more stimulating, because two main elements of courtship behaviour increased in frequency. In every type of mating both selected *e* and selected *vg* males showed more "licking" (i.e. licking the female's genitalia by the male) and selected *e* males also showed more "licking and vibration" (a wing display). Second, selection had changed female behaviour. Females became more choosy by showing repelling behaviour more frequently in hybrid matings. Selection did not change the behaviour of females towards their own males. Outcrossed females, on the contrary, did not repel the two kind of males differently. In conclusion, the changed mating behaviour of the selected lines was mainly caused by changes in female mating preference, whereas changed male behaviour contributed to faster mating.

The third behaviour-genetic investigation on female mating preference studied the preference for *yellow* males relative to wild-type

males (HEISLER, 1984). This study aimed to study in detail the genetic variation in female mating preference between different wild-type laboratory populations of *Drosophila melanogaster* with the aid of a Mendelian breeding scheme.

*yellow* (*y*) Is a recessive, sex-linked mutation which causes a yellow body coloration in males and homozygous females. *y* Has also pleiotropic effects on components of male courtship that are known to be important in stimulating females to accept courtship. Therefore, in this case female mating preference for *yellow* males does not result in a net preference for *yellow*: wild-type males were always more successful at courting females than were *yellow* males. Heisler compared

TABLE I

Investigated Mendelian crosses and their genetic constitution of two *Drosophila melanogaster* strains from which females relatively frequently (H) and rarely (L) mated with *yellow* males, respectively. After HEISLER, 1984.

| *Cross* (♀ × ♂) | *Origin of cytoplasm* | *Expected proportion of H chromosomes* | |
|---|---|---|---|
| | | *X* | *autosomes* |
| 1. H × H | H | 2 | 2 |
| 2. H × $F_1$(H × L) | H | 2 | 1.5 |
| 3. H × $F_1$(L × H) | H | 1 | 1.5 |
| 4. H × L | H | 1 | 1 |
| 5. L × H | L | 1 | 1 |
| 6. L × $F_1$(H × L) | L | 1 | 0.5 |
| 7. L × $F_1$(L × H) | L | 0 | 0.5 |
| 8. L × L | L | 0 | 0 |
| 9. $F_1$(H × L) × $F_1$(H × L) | H | 1.5 | 1 |
| 10. $F_1$(L × H) × $F_1$(H × L) | L | 1.5 | 1 |
| 11. $F_1$(H × L) × $F_1$(L × H) | H | 0.5 | 1 |
| 12. $F_1$(L × H) × $F_1$(L × H) | L | 0.5 | 1 |

female mating preference of two wild-type laboratory strains; females from one strain (H) mated relatively frequently with *y* males, while those from the other (L) rarely mated with *y* males. Female mating preference was measured in mating chambers containing virgin females and males of two "tester" strains, namely a wild-type and a *yellow* strain. Copulating pairs were removed and phenotype of the male was recorded.

Comparisons of the appropriate crosses (see table I) yielded information on maternal effects versus Mendelian inheritance, X-linked

versus autosomal factors, and the presence or absence of dominance. Amongst all crosses there was significant variation in female mating preference. There were 13 pairs of crosses in which two of the three components of inheritance (see table I) were constant while the third varied. Analysis of the reciprocal $F_1$ and $F_2$ crosses (4-5, 9-10, 11-12) did not reveal cytoplasmic or environmental maternal effects. Among the comparisons to reveal X-chromosome effects significant differences were found between 2-3 and the pooled data of 9-4 and 10-5. This indicates a phenotypic difference between females homozygous for the H X-chromosome and females heterozygous for the two strains. Females homozygous for the L X-chromosome had the same mating preference as heterozygotes, namely 0. These results suggest that the X-chromosomal factors that increase female choice for *yellow* males act in a net recessive manner. Amongst the comparisons to reveal autosomal effects a significant difference was found between 7-8. This suggests that autosomal loci also contribute to the strain difference. Also the great difference between $F_1$ flies and the L parent, which cannot be accounted for by X-linked factors (since the effect of the X-chromosome on mate choice was smaller) points to the involvement of autosomal factors that, in heterozygous condition, exhibit overdominance for increased female mating preference to *yellow* males.

By analysing the sequential pattern of mating within individual tests, HEISLER (1984) was able to show that the difference between H and L females was not simply a difference in their overall willingness to mate, but in the probability that they will mate with a *yellow* male, given that they are mating. If the difference reflected a difference in overall receptivity of H and L females, then the mating rate of *yellow* males in competition with wild-type males should be the same during early matings with both types of females. However, *yellow* males were more successful during early mating with H females than with L females. This confirm that mating preference contributed, at least in part, to the difference between H and L females.

### *Cockroaches*

In a recent study, MOORE (1989) analysed father-daughter comparisons of female preference for olfactory cues associated with dominance status in the cockroach *Nauphoeta cinerea*. The results suggested the presence of a positive genetic correlation between female mating preference and preferred male trait and were indicative for the presence of genetic variation in female mating preference.

## FEMALE MATING PREFERENCES AND SEXUAL IMPRINTING

An interesting alternative view of the evolution of exaggerated sexual ornaments in males was recently offered by TEN CATE & BATESON (1988). As opposed to nearly all models of sexual selection and the experimental evidence for genetic variation in female mating preference, this view puts learning processes forward as the most important determinants of female mating preferences. In many precocial bird species, but also in altricial ones, mating preferences for particular types of plumage develop as a result of imprinting, which depends on exposure to that plumage early in life. This learning process is known as sexualimprinting (*e.g.* IMMELMAN, 1972) and ethologists have paid much attention to the causal mechanisms underlying this process (*e.g.* TEN CATE, 1989). The functional significance of sexual imprinting was made clear in experiments by BATESON (1978a, 1980, 1982, 1983) on Japanese quail (*Coturnix coturnix*). Although the learning process may operate in both sexes, I will concentrate on its role on female mating preference. Female Japanese quail did not prefer males with identical plumage characteristics as the conspecifics to which they had been exposed early in life, but rather those males that were slightly different, though not extremely so. Japanese quail females reared with siblings early in life and offered a choice when they were sexually mature between males with various degrees of relatedness, preferred first cousins over familiar siblings, novel siblings, third-cousins and unrelated males. This mating preference for slightly novel mates, as the net outcome of two learning processes, *i.e.* sexual imprinting and habituation, leads to avoidance of inbreeding and thereby of the well-known deleterious effects associated with it. TEN CATE & BATESON (1988) argued that if the female mating preference for slightly novel males is asymmetric in the direction of greater conspicuousness, this might lead to the evolution of exaggerated sexual ornaments in males. This asymmetry was evinced in experiments on Japanese quail that were individually exposed to one of three different types of imprinting stimuli early in life (TEN CATE & BATESON, 1989). The imprinting stimuli were adult white male or female quail with zero, three or six black dots painted on their breast feathers. After a period of visual isolation the (in this case unfortunately male) mating preference of the birds was tested for the familiar number of dots or fewer or more dots in a simultaneous three-way choice test by confining the test male in the center of a circular arena and recording the time spent near each stimulus bird surrounding it. Two series were run in which the stimulus birds differed from each other in either one to two or three to six spots. Both series

gave similar results and showed that adult quail preferred birds with the largest number of dots.

Such a preference for "supernormal" stimuli is widespread, not only for secondary sexual characters, and may be a conservative design feature of many nervous systems. The possibility that female mating preference for supernormal stimuli can lead to the evolution of exaggerated sexual ornaments in males has been considered several times (*e.g.* BORGIA, 1987; KIRKPATRICK, 1987b) and leads us back to Darwin's "aesthetic" view on sexual selection. What is novel about TEN CATE & BATESON's (1988) hypothesis is the coupling of female mating preference for supernormal stimuli and sexual imprinting. It might be questioned, however, whether this process alone can lead to exaggerated male ornaments. First, because both the preference for supernormal stimuli and the process of sexual imprinting happen to be not sex-limited, although it would pay to look for differences between the sexes in these respects. A comparative study of the correlation between the importance of female mate choice relative to male mate choice and the degree of sexual dimorphism could give some indication. Second, although female mating preference for novel stimuli is directional for exaggeration, it may not at all be consistent for particular exaggerated male traits.

Knowledge of the involvement of genetic variation both in the preference for supernormal stimuli and in sexual imprinting is crucial for judging how much established sexual selection models, in which genetic variation of female mating preference is an important premise, differ from models in which female mating preference is learned or culturally inherited. I do not know of any behaviour-genetic studies on sexual imprinting, but research by KOVACH (*e.g.* KOVACH, 1979, 1980, 1990; KOVACH & WILSON, 1988) on filial imprinting in Japanese quail impressively illustrates this point. Although the two processes of filial and sexual imprinting are thought to be at least partially distinct (*e.g.* BATESON, 1978b), early experience in a sensitive period that leads to an early social bond (process of filial imprinting) can influence subsequent choice of a sexual partner. Newly hatched quail chicks tend to approach conspicuous visual stimuli. Interestingly, they exhibit distinct preferences between stimulus colours. Colour preference tests were done on 27 h old individuals without visual experience prior to testing. KOVACH used a 14-choice binary mass-screening apparatus of a similar design as the mass-screening mazes used for *Drosophila* (HIRSCH, 1959). The chicks were released in a starting compartment that, like all other compartments, offered a choice between two stimulus colours at the target end. They could proceed from one into the next compartment through two trap doors in each compartment,

one in front of each stimulus colour, which opened under the weight of the chick as it closely approached a particular stimulus colour. After 7 trials the chicks ended up in a collection box, the position of which indicated the number of times one stimulus colour had been chosen over another. Chicks were tested in two consecutive runs through the apparatus, giving maximum scores of 14. The mass-screening allowed for the study of large numbers of individuals, which is a prerequisite for a proper behaviour-genetic analysis and for an effective selection programme, especially because the quail is unusually sensitive to inbreeding depression.

Chicks were tested for unconditional choices between blue and red stimuli. In the base population the level of preference varied greatly. Twenty generations of artificial selection for blue or red preferences resulted in nearly absolute mean preferences in both lines and strongly reduced phenotypic variation within the selection lines. Thus, to some extent individual variations in the quail's unconditional colour preferences were genetic in origin.

The level of these unconditional colour preferences were to some extent modifiable by learning (*i.e.* imprinting to alternate colours). Twelve hours of perceptual imprinting to blue or red of unselected birds increased the probability that the exposure stimulus was chosen over another stimulus (fig. 3; control line). In birds that had been selected for unconditional red or blue preference, imprinting to the preferred colours barely increased the probability of choosing those colours. Imprinting the selected birds to the unpreferred colours resulted in significant changes in mean preference (fig. 3; red and blue lines). Note that imprinting to unpreferred colours did not reverse the genetically selected unconditional colour preference. These results suggest an additive interaction of unlearned and learned responses.

The genetic influences in unconditional colour choices are not the only route through which genetic factors may influence perceptual imprinting. This was shown in other selection experiments on Japanese quail. Selection for imprintability to blue or red colours after 12 hours perceptual imprinting to the blue or red stimulus resulted in significant changes in the imprintability of chicks to red and blue colours (KOVACH, 1979). Every generation chicks of both selection lines were also tested for imprintability by cross-exposure to the colour not favoured in selection and for unconditional choices between colours. The effects of selection appeared readily transferable from the colour favoured to the colour not favoured in selection. Selection also resulted in bidirectional changes, though small, in the unconditional choices between blue and red. In addition bidirectional selection was exerted on the extent to which unconditional preference for one colour (red or

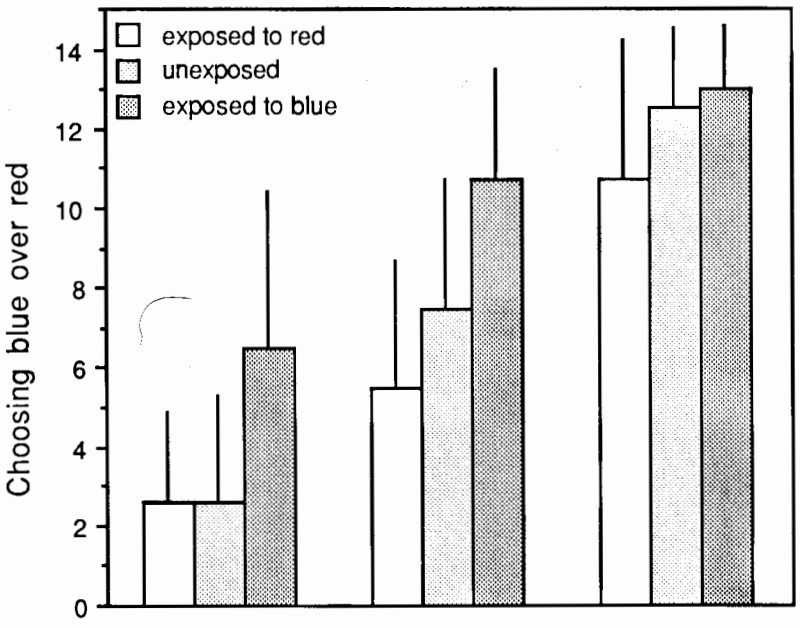


Fig. 3. Mean number of times of choosing blue over red in 14 trials (+SD) of Japanese quail chicks selected during 10 generations for unconditional preference of red over blue (red line) or blue over red (blue line) and of unselected chicks (control line) after exposure for 12 hours to either a red, no, or blue stimulus light. After KOVACH, 1979.

blue) and postimprinting preference for another colour (blue or red) differed (KOVACH, 1990). The results were in agreement with the previous selection experiment on imprintability. Analyses of responses, correlated responses, and hybrid performances in the different selection experiments indicated essential differences between the genetic factors affecting unconditional colour choice and imprintability, but an interrelated polygenic regulation of major gene effects in unconditional colour choices and imprintabilities to colours.

Sexual selection models based on learned or culturally inherited female mating preferences cannot circumvent genetic variation in unconditional preferences and imprintability. There is an apparent gap in our knowledge of genetic influences on sexual imprinting. A proper evaluation of the effects of sexual imprinting on the evolution of exaggerated male traits requires the construction of formal models which allow for the interaction of learned and genetic effects on female mating preference.

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## REFERENCES

ANDERSSON, M., 1982. Sexual selection, natural selection and quality advertisment. Biol. J. Linn. **17**: 375-393.

ARNOLD, S. J., 1985. Quantitative genetic models of sexual selection. Experientia **41**: 1296-1310.

BAKKER, Th. C. M., 1986. Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): a behaviour-genetic study. Behaviour **98**: 1-144.

BAKKER, Th. C. M. & P. SEVENSTER, 1983. Determinants of dominance in male sticklebacks (*Gasterosteus aculeatus* L.). Behaviour **86**: 55-71.

BATESON, P., 1978a. Sexual imprinting and optimal outbreeding. Nature **273**: 659-660.

BATESON, P., 1978b. Early experience and sexual preferences. In: J. HUTCHISON (Ed.): *Biological Determinants of Sexual Behaviour:* 29-53. John Wiley & Sons, Chichester, England.

BATESON, P., 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. Z. Tierpsychol. **53**: 231-244.

BATESON, P., 1982. Preferences for cousins in Japanese quail. Nature **295**: 236-237.

BATESON, P., 1983. Optimal outbreeding. In: P. BATESON (Ed.): *Mate Choice:* 257-277. Cambridge University Press, Cambridge.

BAUERNFEIND, J. C., G. B. BRUBACHER, H. M. KLAUI & W. L. MARUSICH, 1971. Use of carotenoids. In: O. ISLER (Ed.): *Carotenoids:* 743-770. Birkhauser Verlag, Basel.

BISCHOFF, R. J., J. L. GOULD & D. I. RUBENSTEIN, 1985. Tail size and female choice in the guppy (*Poecilia reticulata*). Behav. Ecol. Sociobiol. **17**: 253-255.

BORGIA, G., 1987. A critical review of sexual selection models. In: J. W. BRADBURY & M. B. ANDERSSON (Eds.): *Sexual Selection: Testing the Alternatives:* 55-66. John Wiley & Sons, Chichester, England.

BRADBURY, J. W. & M. B. ANDERSSON (Eds.), 1987. *Sexual Selection: Testing the Alternatives.* John Wiley & Sons, Chichester, England.

BRAKEFIELD, P. M., 1984. Selection among clines in the ladybird *Adalia bipunctata* in The Netherlands: a general mating advantage to melanics and its consequences. Heredity **53**: 37-49.

BRAKEFIELD, P. M., 1987. Industrial melanism: do we have the answers? Trends Ecol. Evol. **2**: 117-122.

BRAKEFIELD, P. M. & P. G. WILLMER, 1985. The basis of thermal melanism in the ladybird *Adalia bipunctata:* differences in reflectance and thermal properties between the morphs. Heredity **54**: 9-14.

BREDEN, F. & G. STONER, 1987. Male predation risk determines female preference in the Trinidad guppy. Nature **329**: 831-833.

BRUSH, A. H. & H. M. REISMAN, 1965. The carotenoid pigments in the three-spined stickleback, *Gasterosteus aculeatus.* Comp. Biochem. Physiol. **14**: 121-125.

BURLEY, N., G. KRANTZBERG & P. RADMAN, 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Anim. Behav. **30**: 444-455.

CATE, C. TEN, 1989. Behavioral development: towards understanding processes. In: P. P. G. BATESON & P. H. KLOPFER (Eds.): *Perspectives in Ethology, Vol. 8:* 243-269. Plenum Press, New York.

CATE, C. TEN & P. BATESON, 1988. Sexual selection: the evolution of conspicuous characteristics in birds by means of imprinting. Evolution **42**: 1355-1358.

CATE, C. TEN & P. BATESON, 1989. Sexual imprinting and a preference for 'supernormal' partners in Japanese quail. Anim. Behav. **38**: 356-358.

CRAIK, J. C. A., 1985. Egg quality and egg pigment content in salmonid fishes. Aquaculture **47**: 61-88.

CRONLY-DILLON, J. & S. C. SHARMA, 1968. Effect of season and sex on the photopic spectral sensitivity of the three-spined stickleback. J. exp. Biol. **49**: 679-687.

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.

DARWIN, C., 1871. *The Descent of Man, and Selection in Relation to Sex.* John Murray, London.

ENDLER, J. A., 1978. A predator's view of animal color patterns. In: M. K. HECHT, W. C. STEERE & B. WALLACE (Eds.): *Evolutionary Biology, Vol. 11:* 319-364. Plenum Publishing Corporation, New York.

ENDLER, J. A., 1980. Natural selection of color patterns in *Poecilia reticulata*. Evolution **34**: 76-91.

ENDLER, J. A., 1983. Natural and sexual selection on color patterns in poeciliid fishes. Env. Biol. Fish. **9**: 173-190.

ENDLER, J. A., 1987. Predation, light intensity and courtship behaviour in *Poecilia reticulata* (Pisces: Poeciliidae). Anim. Behav. **35**: 1376-1385.

ENDLER, J. A., 1988. Sexual selection and predation risk in guppies. Nature **332**: 593-594.

FARR, J. A., 1975. The role of predation in the evolution of social behavior of natural populations of the guppy *Poecilia reticulata* (Pisces: Poeciliidae). Evolution **29**: 151-158.

FARR, J. A., 1977. Male rarity or novelty, female choice behavior, and sexual selection in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae). Evolution **31**: 162-168.

FARR, J. A., 1980. Social behaviour patterns as determinants of reproductive success in the guppy, *Poecilia reticulata* Peters (Pisces: Poeciliidae). An experimental study of the effects of intermale competition, female choice and sexual selection. Behaviour **74**: 38-91.

FISHER, R. A., 1930. *The Genetical Theory of Natural Selection.* Clarendon Press, Oxford.

FISHER, R. A., 1958. *The Genetical Theory of Natural Selection (2nd ed.).* Dover Publications, New York.

HAMILTON, W. D. & M. ZUK, 1982. Heritable true fitness and bright birds: a role for parasites? Science **218**: 384-387.

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

HEISLER, L., M. B. ANDERSSON, S. J. ARNOLD, C. R. BOAKE, G. BORGIA, G. HAUSFATER, M. KIRKPATRICK, R. LANDE, J. MAYNARD SMITH, P. O'DONALD, A. R. THORNHILL & F. J. WEISSING, 1987. The evolution of mating preferences and sexually selected traits. Group report. In: J. W. BRADBURY & M. B. ANDERSSON (Eds.): *Sexual Selection: Testing the Alternatives:* 96-118. John Wiley & Sons, Chichester, England.

HERT, E., 1986. Freeze branding in fish, a method for eliminating colour patterns at the skin surface. Ethology **72**: 165-167.

HERT, E., 1989. The function of egg-spots in an African mouth-brooding cichlid fish. Anim. Behav. **37**: 726-732.

HIRSCH, J., 1959. Studies in experimental behaviour genetics. II. Individual differences in geotaxis as a function of chromosome variations in synthesized *Drosophila* populations. J. Comp. Physiol. Psychol. **52**: 304-308.

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

HOUDE, A. E., 1988a. Genetic differences in female choice between two guppy populations. Anim. Behav. **36**: 510-516.

HOUDE, A. E., 1988b. Sexual selection in guppies called into question. Nature **333**: 711.

HOUDE, A. E. & J. A. ENDLER, 1990. Correlated evolution of female mating preferences and male color patterns in the guppy *Poecilia reticulata*. Science **248**: 1405-1408.

IMMELMAN, K., 1972. The influence of early experience upon the development of social behaviour in estrildine finches. In: K. H. VOOUS (Ed.): *Proceedings of the XV International Ornitological Congress, Den Haag, 1970:* 316-338. Brill, Leiden, Netherlands.

JOACHIM, D. & D. J. W. CURTSINGER, 1990. Genotype and anesthetic determine mate choice in *Drosophila melanogaster*. Behav. Genet. **20**: 73-79.

KENNEDY, C. E. J., J. A. ENDLER, S. L. POYNTON & H. MCMINN, 1987. Parasite load predicts mate choice in guppies. Behav. Ecol. Sociobiol. **21**: 291-295.

KIRKPATRICK, M., 1982. Sexual selection and the evolution of female choice. Evolution **30**: 1-12.

KIRKPATRICK, M., 1987a. Sexual selection by female choice in polygynous animals. Ann. Rev. Ecol. Syst. **18**: 43-70.

KIRKPATRICK, M., 1987b. The evolutionary forces acting on female mating preferences in polygynous animals. In: J. W. BRADBURY & M. B. ANDERSSON (Eds.): *Sexual Selection: Testing the Alternatives:* 67-82. John Wiley & Sons, Chichester, England.

KODRIC-BROWN, A., 1985. Female preference and sexual selection for male coloration in the guppy (*Poecilia reticulata*). Behav. Ecol. Sociobiol. **17**: 199-205.

KODRIC-BROWN, A., 1989. Dietary carotenoids and male mating success in the guppy: an environmental component to female choice. Behav. Ecol. Sociobiol. **25**: 393-401.

KOVACH, J. K., 1979. Genetic influences and genotype-environment interactions in perceptual imprinting. Behaviour **68**: 31-60.

KOVACH, J. K., 1980. Mendelian units of inheritance control color preferences in quail chicks (*Coturnix coturnix japonica*). Science **207**: 549-551.

KOVACH, J. K., 1990. Nonspecific imprintability of quail to colors: response to artificial selection. Behav. Genet. **20**: 91-96.

KOVACH, J. K. & G. WILSON, 1988. Genetics of color preferences in quail chicks: major genes and variable buffering by background genotype. Behav. Genet. **18**: 645-661.

LANDE, M., 1981. Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci. **78**: 3721-3725.

LONG, K. D. & 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. & N. R. LILEY, 1985. Geographic variation in the sexual behaviour of the guppy, *Poecilia reticulata* (Peters). Behaviour **95**: 164-179.

MAGURRAN, A. E. & B. H. SEGHERS, 1989. Risk sensitive courtship in the guppy (*Poecilia reticulata*). Behaviour **112**: 194-201.

MAJERUS, M. E. N., 1986. the genetics and evolution of female choice. Trends Ecol. Evol. **1**: 1-7.

MAJERUS, M. E. N., P. O'DONALD, P. W. E. KEARNS & H. IRELAND, 1986. Genetics and evolution of female choice. Nature **321**: 164-167.

MAJERUS, M. E. N., P. O'DONALD & J. WEIR, 1982a. Female mating preference is genetic. Nature **300**: 521-523.

MAJERUS, M., P. O'DONALD & J. WEIR, 1982b. Evidence for preferential mating in *Adalia bipunctata*. Heredity **49**: 37-49.

MARLER, C. A. & M. C. MOORE, 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. Behav. Ecol. Sociobiol. **23**: 21-26.

MAY, R. M. & R. M. ANDERSON, 1983. Epidemiology and genetics in the coevolution of parasites and hosts. Proc. R. Soc. Lond. **B 219**: 281-313.

MAYNARD SMITH, J., 1985. Mini review: sexual selection, handicaps and true fitness, J. theor. Biol. **115**: 1-8.

MAYNARD SMITH, J., 1987. Sexual selection - a classification of models. In: J. W. BRADBURY & M. B. ANDERSSON (Eds.): *Sexual Selection: Testing the Alternatives:* 9-20. John Wiley & Sons, Chichester, England.

MCLENNAN, D. A., D. R. BROOKS & J. D. MCPHAIL, 1988. The benefits of communication between comparative ethology and phylogenetic systematics: a case study using gasterosteid fishes. Can. J. Zool. **66**: 2177-2190.

MCLENNAN, D. A. & J. D. MCPHAIL, 1989. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): temporal changes in the structure of the male mosaic signal. Can. J. Zool. **67**: 1767-1777.

MCLENNAN, D. A. & J. D. MCPHAIL, 1990. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): the relationship between male colour and female behaviour. Can. J. Zool. **68**: 482-492.

MCPHAIL, J. D., 1969. Predation and the evolution of a stickleback (*Gasterosteus*). J. Fish. Res. Bd. Canada **26**: 3183-3208.

MILINSKI, M. & Th. C. M. BAKKER, 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. Nature **344**: 330-333.

MOLAN, A. L., P. F. BRAIN & B. L. JAMES, 1984. The retention and egg production in *Microphallus pygmaeus* (Levinsen, 1881) (Digenea: Microphallidae) in gonadectomized and hormone-treated male mice. Z. Parasitenkd. **70**: 627-636.

MØLLER, A. P., 1988. Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature **332**: 640-642.

MOODIE, G. E. E., 1972. Predation, natural selection and adaptation in an unusual threespine stickleback. Heredity **28**: 155-167.

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

NAKANISHI, H., Y. HORII, K. TERASHIMA & K. Fujita, 1989. Effect of testosterone on the susceptibility of C57BL/6 mice to infection with *Brugia pahangi* with reference to inflammatory cell response. J. Parasitol. **75**: 455-460.

O'DONALD, P., 1962. The theory of sexual selection. Heredity **17**: 541-552.

O'DONALD, P., 1967. A general model of sexual and natural selection. Heredity **22**: 499-518.

O'DONALD, P., M. DERRICK, M. MAJERUS & J. WEIR, 1984. Population genetic theory of the assortative mating, sexual selection and natural selection of the two-spot ladybird, *Adalia bipunctata*. Heredity **52**: 43-61.

O'Donald, P. & M. E. N. Majerus, 1984. Polymorphism of melanic ladybirds maintained by frequency-dependent sexual selection. Biol. J. Linn. Soc. **23**: 101-111.

O'Donald, P. & M. E. N. Majerus, 1985. Sexual selection and the evolution of preferential mating in ladybirds. I. Selection for high and low lines of female preference. Heredity **55**: 401-412.

Partridge, L., 1989. Frequency-dependent mating preferences in female fruitflies? Behav. Genet. **19**: 725-728.

Pelkwijk, J. J. ter & N. Tinbergen, 1937. Eine reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. Z. Tierpsychol. **1**: 193-200.

Pomiankowski, A. N., 1988. The evolution of female mate preferences for male genetic quality. In: P. H. Harvey & L. Partridge (Eds.): *Oxford Surveys in Evolutionary Biology, Volume 5:* 136-184. Oxford University Press, Oxford.

Read, A. F., 1988. Sexual selection and the role of parasites. Trends Ecol. Evol. **3**: 97-102.

Reimchen, T. E., 1989. Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). Evolution **43**: 450-460.

Reisman, H. M., 1968. Effects of social stimuli on the secondary sex characters of male three-spined sticklebacks, *Gasterosteus aculeatus*. Copeia **1968**: 816-826.

Rowland, W. J., 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). Behav. Ecol. Sociobiol. **24**: 433-438.

Schantz, T. von, G. Göransson, G. Andersson, I. Fröberg, M. Grahn, A. Helgée & H. Wittzell, 1989. Female choice selects for a viability-based male trait in pheasants. Nature **337**: 166-169.

Seger, J., 1985. Unifying genetic models for the evolution of female choice. Evolution **39**: 1185-1193.

Segner, H., P. Arend, K. von Poeppinghausen & H. Schmidt, 1989. The effect of feeding astaxanthin to *Oreochromis niloticus* and *Colisa labiosa* on the histology of the liver. Aquaculture **79**: 381-390.

Semler, D. E., 1971. Some aspects of adaptation in a polymorphism for breeding colours in the Threespine stickleback (*Gasterosteus aculeatus*). J. Zool., Lond. **165**: 291-302.

Spiess, E. B. & L. Ehrman, 1978. Rare male mating advantage. Nature **272**: 188-189.

Stoner, G. & F. Breden, 1988. Phenotypic differentiation in female preference related to geographic variation in male predation risk in the Trinidad guppy (*Poecilia reticulata*). Behav. Ecol. Sociobiol. **22**: 285-291.

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

Tomlinson, I. & P. O'Donald, 1989. The co-evolution of multiple female mating preferences and preferred male characters: the "gene-for-gene" hypothesis of sexual selection. J. theor. Biol. **139**: 219-238.

Wootton, R. J., 1976. *The Biology of the Sticklebacks.* Academic Press, London.

Wunder, W., 1934. Gattenwahlversuche bei Stichlingen und Bitterlingen. Zool. Anz. Suppl. **7**: 152-158.

Zahavi, A., 1975. Mate selection - a selection for a handicap. J. theor. Biol. **53**: 205-214.