The Rare-Male Effect: What is Its Evolutionary Significance?

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The rare-male effect: what is its evolutionary significance?

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Negatively frequency-dependent male mating success, the rare-male effect (RME), has been reported from many laboratory experiments, particularly with *Drosophila* spp. Problems with observer bias, lack of repeatability, with experimental design and with the analysis of data may indicate that the RME is considerably less well documented than has been supposed, even in the laboratory. Male competition is unlikely to be a common cause of the RME, except where there are behavioural differences between competing strains that result in lower competition between them than within them. A mixture of fixed female preferences seems the most likely cause, and further behavioural studies are required to investigate this mechanism. There is no convincing evidence that the RME is a consequence of frequency-dependent female preferences. An RME in the absence of negative assortment is not in general expected to lead to the avoidance of inbreeding because matings between relatives will not be reduced. Nor is it likely to contribute to the high levels of genetic polymorphism found in nature, because females would be required to base their mating preferences on genotypes at all or most loci, to show individual variation in respect of their preferences and to sum the information into an index of genomic rarity. Given the levels of polymorphism involved, all males are likely to be rare by some criterion. A varying direction of female preference, required for a two-sided RME and for the maintenance of genetic polymorphism, has yet to be reported from wild populations. The RME is therefore probably of limited evolutionary significance. Disassortative mating with respect to self-incompatibility alleles in plants, and possibly major histocompatibility complex (MHC) alleles in vertebrates, results in an RME, inbreeding avoidance and high levels of genetic polymorphism at these loci.

INTRODUCTION

The phenomenon

Male mating success is an important component of fitness. Lifetime mating success can be highly variable (see, for example, Prout 1971; Bundgaard & Christiansen 1972; Anderson *et al.* 1979; Clutton-Brock *et al.* 1982; Partridge & Farquhar 1983; Banks & Thompson 1985) and is often related to characters such as large body size (see, for example, Clutton-Brock *et al.* 1982; Partridge & Farquhar 1983; Partridge *et al.* 1987) and elaborate ornamentation (see, for example, Andersson 1982; Endler 1983; Catchpole *et al.* 1984; Borgia 1985; Houde 1987). Directional sexual selection is therefore implied in these cases.

Frequency-dependent sexual selection, where the mating success of an individual male varies with the frequency of its morph in the male population, has also been often reported (reviewed in Partridge & Hill 1984; Knoppien 1985). The frequency-dependence is in general negative. The relative mating success of two strains of males can be defined by the cross product ratio (CPR):

$$\frac{(A \text{ males mating}) \times (B \text{ males present})}{(A \text{ males present}) \times (B \text{ males mating})}.$$

A change in this ratio so that it declines as the frequency of A males in the male population increases is also known as the rare-male effect (RME). In general the mating success of females is unrelated to their frequency (but see Fontdevila & Mendez 1979). The RME has received considerable attention in the scientific literature and in textbooks because of its suggested potential for maintaining genetic polymorphisms in nature without any genetic load at equilibrium. However, RMES are often one-sided, with one morph having an overall mating advantage at all frequencies, and with the extent of its advantage declining with increasing frequency (see O'Donald & Majerus, this symposium). In general this type of frequency-dependence cannot maintain polymorphism, and a two-sided effect, where the net mating advantage switches from one morph to the other at some intermediate frequency, is necessary (unless countervailing selection on a different fitness component acts to balance the system).

The RME has been reported in laboratory studies of the guppy *Poecilia reticulata* (Farr 1977), the flour beetle *Tribolium castaneum* (Sinnock 1970; but see Wool 1967, 1970), the wasp *Nasonia* (=*Mormoniella*) *vitripennis* (Grant *et al.* 1974), and the two spot ladybird *Adalia bipunctata* (Majerus *et al.* 1982*a*). The melanic and typical forms of the ladybird also show an RME between different field populations in Britain (Muggleton 1979) but not in Holland (Brakefield 1984). The RME has been most often found in laboratory studies of *Drosophila* species, and here a very wide range of differences between competing strains has been reported to produce the phenomenon. Different geographical strains (see, for example, Ehrman & Petit 1968; Spiess & Spiess 1969), inbred lines (Tardif & Murnik 1975), inversion karyotypes (see, for example, Ehrman & Spiess 1969; Klobutcher 1977), enzyme variants (Ehrman *et al.* 1977; Fontdevila & Mendez 1979) and strains carrying visible mutants (see, for example, Petit & Nouaud 1975; Spiess & Schwer 1978; Spiess & Kruckeberg 1980), as well as the same strain reared at different temperatures (Ehrman 1966), on different media (Dal Molin 1979) or taken from different positions in the storage bottle (Markow 1980), have all been reported to show an RME.

Some problems with data, procedure and analysis

Studies where an RME has been sought but not found have been reported (see, for example, Klobutcher 1977; Anderson & McGuire 1978; Markow 1978; Markow *et al.* 1980; Pot *et al.* 1980; Partridge & Gardner 1983; Oberhauser 1988) and many have not been reported (various workers, personal communication). There may therefore be a considerable bias in the literature.

There have also been some problems with the design of experiment and the analysis of data. For instance, in the mass-mating experiments typically used in the *Drosophila* studies, some workers vary male frequency only, whereas others vary male and female frequency together. Moreover, in some studies, pairs are removed as they mate whereas in others they are not, so that the male, and to a lesser extent the female, may mate for a second time. Some experiments are run for a fixed time, others for a fixed number of matings. These different designs require different types of analysis, and may produce any RME found by different mechanisms. The statistics applied to them have often been inappropriate (Partridge & Hill 1984; Knoppien 1985), and in some cases the reanalysis of earlier data has caused a reported RME to disappear (Merrell 1983; Knoppien 1985). Lastly, in many rare-male experiments in *Drosophila*, morphologically indistinguishable strains are marked by wing-clipping. If the mating success of males is affected by this procedure, as might be expected because reduced wing area has been demonstrated to lower male mating success (Ewing 1964), then the RME may appear as an artefact of the marking procedure (Kence 1981, 1986; Knoppien 1984).

MECHANISMS FOR THE RME

Frequency-dependent female choice?

Several mechanisms for the RME have been put forward. A common proposal is that the RME is a consequence of frequency-dependent mate choice by females; they are suggested to sample the male population, assess the frequencies of different male morphs, and bias their mating preferences towards the least common male types, possibly as a result of sensory habituation to cues produced by the more common types (Spiess 1968; Ehrman & Spiess 1969). Such behaviour by females has been suggested to function as an outbreeding mechanism; assuming gene frequencies are approximately equal in males and females, then an individual female will on average be most likely to carry a common genotype, and by mating with a rare male she will therefore tend to mate disassortatively with respect to the criteria on which her mate choice is based (Lacy 1979; Grant *et al.* 1980; Searcy 1982). There are several problems with this suggestion. The first is that, because of the very large array of genetic and environmental differences between strains that have been reported to be capable of producing the RME (see above), every male must be rare by some criterion. The sensory systems of a female insect would be greatly taxed to assess so many phenotypic characters and to produce some sort of summary. This problem becomes more acute if the RME is to be implicated in maintaining the numerous genetic polymorphisms found in nature, because the preferred male would carry common genotypes for at least some loci. In addition, locally rare genotypes are likely to be new mutants or immigrants, both of which will probably suffer a disadvantage under natural selection, so that for this reason there should be selection against a preference for male rarity. Moreover, outbreeding could be achieved far more simply if the females were to mate disassortatively with respect to their own phenotype, rather than mating with rare males.

The evidence for frequency-dependent female preferences has come from two types of experiment. The first involved observations, using single females, of courtship sequences and matings by males of different genotypes. In most experiments these were eye-colour mutants of *D. melanogaster*, and by using these in both mass mating tests and experiments with single females courted by groups of males, an RME was found (Spiess & Schwer 1978; Spiess & Kruckeberg 1980; Spiess 1982*a*). In addition, tests with single females were thought to show that the females became biased against males of the first genotype to court them; females first courted by brown-eyed males were more likely to go on to mate with an orange-eyed male, whereas females first courted by orange-eyed males were then more likely to mate with brown-eyed males (Spiess 1982*b*; Spiess & Bowbal 1987). Such behaviour would be consistent with the notion that females habituate to cues from the first male to court, and become less receptive to them in consequence. It would also provide a basis for the RME, because males of a particular genotype are more likely to be the first to court when that genotype is more common in the male population.

There was one problem of design in these observations of single females. All trials in which the female was courted by males of only one genotype before mating were discarded from the analysis on the grounds that the female had not had a chance to sample the male population before mating. This procedure introduces three biases. First, discarding trials produces a serious statistical artefact. To illustrate this, suppose that females are courted twice, mating with the male that delivers the second courtship. Four courtship sequences are possible, namely brown–brown, brown–orange, orange–brown, orange–orange. The first and the last results will be discarded before the analysis, so that 100% bias against males of the first genotype to court will be observed solely as an artefact of the procedure. As the total number of courtships increases, the extent of this bias will decline, but data on the number of courtships delivered (Spiess & Kruckeberg 1980) make it clear that it is likely to be serious. Second, if female preference for the two types of males is individually variable, then by discarding females that mate with a male of the first genotype to court with them, one may be discarding females with a particularly strong preference for that male genotype. The residual sample of females left for inclusion in the analysis may therefore consist of individuals which from the start had a relatively low preference for males of that genotype. Third, if males vary in courtship vigour, courtship by males of only a single genotype before mating may reflect the presence of particularly vigorous males of that genotype, and discarding the chambers involved will leave a residue of the less vigorous. For all these reasons, it is essential that data from all mating chambers be included in the final analysis. Reanalysis of the earlier data (Partridge & Gardner 1983) showed that inclusion of discarded chambers in one study (Spiess & Kruckeberg 1980) did not remove either the rare-male effect or female avoidance of the first male to court, but caused the avoidance to turn into a preference in a subsequent set of data (Spiess 1982*b*), a finding that also applies to the results of a later study (Spiess & Bowbal 1987). Repetition of the experiments produced no evidence for the RME either mass matings (Partridge & Gardner 1983) or in tests with single females (Oberhauser 1988), and a highly significant tendency for females to mate with males of the first genotype to court them in tests with single females when all data are included in the analysis (Partridge & Gardner 1983). The latter result probably reflects individual variation between males in levels of their success in courtship, and hence in mating. There is therefore no compelling reason to accept the claim for frequency-dependent female choice based on this experimental material.

The second line of evidence for frequency-dependent female preferences came from experiments on pheromones in olfactometers; it was claimed that if air that had first been passed over males in an adjacent chamber was then passed over the flies in a mass mating experiment, the rare males in the experiment lost some or all of their mating advantage if the males in the adjacent chamber were of the same strain. This was claimed to occur in both *D. melanogaster* (Ehrman 1966, 1969, 1970) and *M. vitripennis* (White & Grant 1977). Such a result is consistent with the idea that females habituate to pheromones present in high concentrations, and are hence more receptive to morphs with rare pheromones. A problem with this claim is that it could as easily be the males as the females in the mating chamber that are affected, so the result is not in itself proof of an effect on female preference.

An involvement of a polymorphic pheromone system in mate choice in *Drosophila* has also been claimed by Averhoff & Richardson (1974). Specifically, they suggested that individuals become physiologically and behaviourally unresponsive to their own pheromones, and will therefore not respond to the identical pheromones produced by their close relatives of the opposite sex, so that the system will operate as an outbreeding mechanism. The evidence for this idea was a pattern of increasing negative assortative mating between inbred lines derived from outbred progenitors as inbreeding proceeded. Moreover, they claimed that the difficulty most workers experience in keeping new inbred lines after several generations of inbreeding was caused by failure of mating within lines. The reluctance to mate, they suggested, was specific to flies of the same 'sterile' inbred line, because matings between lines proceeded normally with the production of progeny. In a subsequent study (Averhoff & Richardson 1976) they mapped some of the loci involved to specific chromosomes.

Disassortative mating in *Drosophila* based on a polymorphic pheromone system common to the two sexes has received little support in subsequent studies. One problem is that the data demonstrating negative assortment between inbred lines have not proved repeatable in either *D. melanogaster* (Van den Berg *et al.* 1984; L. Partridge & V. A. Budge, unpublished data) or *D. pseudoobscura* (Powell & Morton 1979). Furthermore, a study examining assortment between lines of outbred *D. melanogaster* differing in their degrees of relatedness also produced negative results (Veuille & Mazeau 1986), whereas the earlier work would predict an excess of matings between lines of lower relatedness. In addition, subsequent work on pheromone chemistry has shown that mature adults of the two sexes do not have pheromones in common (reviewed in Ewing 1983). Another difficulty is that the results of Averhoff & Richardson (1974, 1976) are open to an alternative interpretation proposed by Bryant (1979), based on an earlier model of mating behaviour in flies (Kence & Bryant 1978). These authors pointed out that geographic strains of flies often differ in both the degree of female receptivity and in the vigour of male courtship, and that these two features frequently covary, females of high receptivity being associated with males of low vigour. Under these circumstances, a pattern of negative assortment between lines is likely to be found, because the most probable matings are those between receptive females and vigorous males. Inbred strains often show considerable differentiation in courtship and mating characteristics (see, for example, Connolly *et al.* 1974) and a similar phenomenon could occur. It is therefore necessary to assess female receptivity and male vigour with experiments on assortment between strains. Lastly, the results of all the olfactometer experiments with *Drosophila* are extremely puzzling because of the finding that the pheromones produced by both sexes are long chain hydrocarbons that would not be volatile over distances of more than a very few millimetres (Antony & Jallon 1982; Jallon 1984; Tompkins 1984). This distance is not sufficient to provide a basis for the results of olfactometer tests.

Because of the lack of hard evidence for frequency-dependent female preferences, other simpler mechanisms for the RME should be investigated.

Male competition

Various models of male competition have been considered by Partridge & Hill (1984), and they concluded that two processes could in theory produce an RME. If males of one strain compete more intensely with one another than with males of a competing strain, then an RME could appear. Alternatively, if males of one strain facilitate matings by males of the competing strain, an RME would also result. This second mechanism has not been reported in any RME experiment. For the first process to occur, there needs to be some difference between males of the competing strains in their methods of acquiring access to females. Although such a difference has been recorded in one experiment with *Drosophila* (Petit & Nouaud 1975), this mechanism cannot explain the vast majority of the classical RME data, where behavioural differences between strains do not appear to occur. None the less, the phenomenon may occur in some animals where the possibility of frequency-dependent mating success has not yet been explicitly investigated.

Behavioural ecologists have only recently become interested in differences in behaviour between members of the same species (Maynard Smith 1982). Differences between males in their tactics for acquiring mates have attracted particular attention and, although such cases are unusual, they may well involve an element of frequency-dependent selection. For instance, in several insects and anuran amphibians, some males call to attract females, while other 'satellite' males stay silently nearby and attempt to intercept and mate with the females approaching the caller (Howard 1978; Cade 1979, 1981; Cade & Wyatt 1984). Although frequency-dependence has not yet been tested, it is likely to be operative in these cases, because callers create opportunities for satellites, although if few males call few females will arrive, and calling by satellites may then be favoured. It is probable that any effect would often be one-sided, with callers having an advantage at all frequencies. The reason is that satellite males often appear to be 'making the best of a bad job', because they are smaller than calling males and would probably fare badly in direct competition with them (see, for example, Howard 1978). In these cases the satellite males may be younger than callers, or may have suffered some growth disadvantage, and ontogenetic data are required to investigate this. Different male behaviours could be associated with equal fitnesses if individuals adjust the behaviour they show in relation to that shown by others. Field experiments investigating this possibility would be valuable. In some cases the behavioural polymorphisms clearly have a genetic basis (see, for example, Cade 1981), which raises the issue of how more than one morph is maintained. Data on both the exact genetic basis of the polymorphisms and on lifetime mating success of the different male morphs are also needed; depending upon the genetic system, equal lifetime reproductive success for different morphs might be predicted if two-sided frequency dependence is maintaining them in the population, whereas the satellites would be expected to have lower fitness than callers if they are making the best of a bad job. However, unequal lifetime mating success for the morphs need not indicate that frequency-dependent selection is not involved, because at equilibrium under frequency-dependent selection equal fitnesses of alternative alleles, and not necessarily of different morphs, is predicted (Maynard Smith 1981).

One case where genetic differences between male morphs do appear to lead to equal lifetime mating success is in the semelparous coho salmon, *Oncorhynchus kisutch*. There are two male morphs known as 'hooknoses' and 'jacks', the former maturing at three and the latter at two years of age. Hooknoses are larger than jacks and fight for access to spawning females, whereas jacks obtain spawnings by stealth. The two morphs appear to have approximately equal lifetime mating success because the greater spawning success of hooknoses that do survive to breed is balanced by a lower likelihood of survival to reproductive maturity (Gross 1985). Two-sided frequency dependence may well occur in this case, but field perturbation experiments would be needed to confirm this.

It thus seems that male competition can lead to frequency-dependent sexual selection, but that such cases are the exception, and the process is unlikely to be operative in most cases where the RME has been reported.

Fixed female preferences

If females exert mating preferences then they are unequally likely to mate with different male morphs when they are encountered. Preferences are fixed or frequency-independent if mating likelihood upon encounter is unaffected by male frequency. Several models of female preferences have shown that if the female population is composed of a mixture of morphs each with different but fixed mating preferences for different male morphs, then an RME can be generated.

The details of the 'female preference rule' vary considerably between models. The simplest but most unrealistic case is one where some females will mate only with males of morph A and the remainder only with morph B; under these circumstances males of the A and B strains will enjoy the same total number of preferential matings at all male frequencies, and there will hence be a strong RME. Female preferences can also be modelled by using the times taken to mating with different male morphs (see, for example, Kence & Bryant 1978) or as mating probabilities. O'Donald (1977, 1978, 1980, 1983) considered the case where females will mate only with their preferred male type during a certain number of encounters, after which, if they have not mated, they do so at random with the next male encountered. These models produce an RME, and also provide a good fit to several RME data sets (O'Donald & Majerus, this symposium). Partridge & Hill (1984) considered the case where females have fixed probabilities of accepting different male morphs, when an RME could appear in both 'single female' and 'mass mating' tests.

It therefore seems that a mixture of fixed female preferences can in theory produce an RME under a wide range of preference rules and experimental designs. This body of theory may well be applicable to many of the RMES reported. For instance, mass mating experiments are often done using a mixture of females from the same strains as the males being tested, and keeping female frequency constant while varying male frequency. Particularly where different geographical, inbred or mutant strains are being tested, the two types of female are likely to differ in mating preferences (Kence & Bryant 1978) and this variation could be responsible for the RME observed. Any variation in female receptivity within or between strains could also produce a one-sided RME if the males of the two strains differ in courtship vigour (Kence & Bryant 1978; Partridge & Hill 1984).

Variation between females in mating preference may also explain the RME in the ladybird *A. bipunctata*, the one species where an effect has been reported from the field. The laboratory data show clearly that two types of female are present in British populations, one with a mating preference for melanics and the other indifferent, with no preference for melanic or typical forms. In addition, the difference in preference appears to be genetic in origin, and attributable to the effects of a single locus or group of closely linked loci (Majerus *et al.* 1982*b*, 1986; O'Donald & Majerus 1985). The reasons for the occurrence of this polymorphism are at present not understood, but its existence would be expected to produce a one-sided RME, as has been found in laboratory studies (O'Donald & Majerus, this symposium). However, it cannot explain the two-sided effect apparently found in earlier studies (Muggleton 1979; O'Donald & Muggleton 1979). These studies were based on lumped data from males and females and different geographical populations, and the occurrence of female preference is known to show geographic variation in this species (Brakefield 1984). Further experiments would therefore be needed to investigate the behavioural basis of the two-sided effect reported in nature.

Disassortative mating preferences

A preference for mates with a dissimilar genotype will lead to disassortative mating, and we have seen that this pattern of mate choice is likely to lead both to avoidance of inbreeding and to polymorphism at the loci involved in producing the disassortment. There is abundant evidence from hermaphrodite and monoecious plants that this mechanism is exploited in various forms of self-incompatibility. Disassortative mating seems to be generally very uncommon in animals (Partridge 1983) including those used in RME experiments, but recent claims for a role of the chordate major histocompatibility complex (MHC) in this context require further investigation.

About half the families of flowering plants have a system of self-sterility based on alleles segregating at one or more loci (see Charlesworth & Charleswoth (1979*a*) for review). The commonest and probably ancestral system is gametophytic, where the pollen expresses its own haploid allele, which must not be identical with either allele in the recipient if successful pollination is to occur. In sporophytic systems the pollen expresses the diploid genotype of its parent plant, and neither allele must be identical with either of those in the recipient. The evolutionary genetics of these systems have been examined by Charlesworth (1979) and Charlesworth & Charlesworth (1979*b*). Assuming that the same allele is responsible for the self-incompatible phenotype in males and females, the condition for a self-incompatible allele to invade a self-fertile system depends largely upon the level of inbreeding depression; if this is high enough, invasion can occur. The spread of the new allele is brought to a halt by negative frequency-dependence, essentially because as the new allele becomes common, the ovules from plants bearing it start to run the risk of failure to receive compatible pollen and hence they suffer lowered female fertility. Further self-incompatible alleles can invade this system. The details of this argument might be considerably altered if different genes are involved in producing the male and female phenotypes. The evidence on this point is not clear. A glycoprotein product cosegregating with the self incompatible phenotype has been identified in females of two species (Nasrallah *et al.* 1985; Anderson *et al.* 1986), but so far no similar substance has been isolated from the pollen. If the two products are identical it seems likely to indicate a mechanism analogous to the self/non-self recognition systems found in animals.

In animals, dispersal before breeding is undoubtedly responsible for much avoidance of inbreeding, especially in small vagile creatures such as *Drosophila*. None the less, there is clear evidence that mating preferences can play a role in the process, often through the avoidance of mating with those individuals or those kinds of individual encountered early in life (Bateson 1983). Any genetic basis for the characters used in this type of recognition could lead to negative frequency-dependence similar to that seen in plant self-incompatibility systems. It has recently been suggested that this type of process could be at least partly responsible both for the evolution and for the extreme genetic polymorphism of the Class I loci of the mammalian MHC (Yamazaki *et al.* 1980), and of a functionally similar locus in a tunicate (Scofield *et al.* 1982).

The mammalian MHC is best known for its role in the rejection of tissue transplants; if a donor allele at the Class I loci is not also held by the host, the transplant is rejected. These loci are extremely polymorphic; in the mouse the *K* and *D* loci have at least 100 alleles each, with 6 additional alleles at the *L* locus. Between them the loci can therefore produce 3.6×10^9 unique Class I phenotypes (Singh *et al.* 1987). An MHC homologue is probably present in all vertebrate classes (Buss & Green 1985). The MHC Class I antigens are cell-surface glycoproteins with a wide tissue distribution. In mammals they are involved in associative recognition of viral antigens; small fragments of foreign antigen become associated with the MHC Class I antigens on the surface of infected cells, and thereby attract the attention of cytotoxic *t* lymphocytes.

Two features of the MHC Class I loci are of particular evolutionary interest. First, why do these loci exist at all, and second why are they so polymorphic? It seems that some sort of functional explanation in terms of balancing selection is necessary to account for the degree of polymorphism, because hypotheses based on neutrality underestimate the heterozygosity for the Class I HLA loci (Hedrick & Thomson 1983; Klitz *et al.* 1984), and strong linkage disequilibrium between some of the loci has also been shown (Bodmer *et al.* 1986).

The role of the MHC in transplant rejection may be based on an earlier evolutionary role in colony fusion in the sessile ancestors of the vertebrates (see, for example, Buss & Green 1985). In many sessile marine invertebrates and lower vertebrates, the ability of colonies to fuse is based on a histocompatibility system, although the genetic and molecular details of the mechanism are usually unknown (see, for example, Hildemann *et al.* 1977, 1979; Lubbock 1980; Stoddart *et al.* 1985; Neigel & Avise 1983, 1985). Fusion may be beneficial to the participants because it produces an increase in size which may confer an advantage in survival or fertility (Scofield *et al.* 1982), and may have resulted in the evolution of a locus allowing the recognition of conspecifics. If this selection pressure were the only one at work, it would be advantageous to be potentially capable of fusion with as many conspecifics as possible, leading to positively frequency-dependent selection at the locus, and a polymorphic histocompatibility system would therefore not be expected to evolve (Crozier 1986). However, the possibility of somatic-cell parasitism in chimeras may have made new rare recognition alleles advantageous, by selectively promoting fusion between related colonies (Buss 1982; Buss & Green 1985). The loss of potential for fusion with a polymorphic system may be to some extent ameliorated by a tendency for mobile larvae to settle near others of a compatible fusibility genotype (Grosberg & Quinn 1986). The role in the rejection of unlike tissues may therefore explain both the initial evolution and the polymorphism of the histocompatibility systems. However, the presence of the system in creatures where this challenge is not naturally encountered requires some other explanation.

At least in mammals, the MHC Class I antigens are involved in the recognition of viral antigens. Unfortunately there is very little information about the role of the MHC in immunity to viral attack among the lower vertebrates, so it is not clear if this role is peculiar to the mammals, or whether it is of greater evolutionary antiquity. The suggestion that the level of MHC Class I polymorphism within the mammals can be explained on the basis of immunity to viral attack does not at present appear particularly convincing. The associations between particular MHC haplotypes and susceptibility to certain diseases, although present (Bodmer 1980, 1984), are weak, and in many cases the diseases involved are not associated with any known infective agent (Klein 1986). Part of the reason for this failure may be the very great recent changes in the spectrum of human diseases (Bodmer 1984), and it might be more profitable to search for such associations in field populations of mice. Of interest here is a recent demonstration with laboratory mice of an association, not necessarily causal, between MHC haplotype and the antibody repertoire produced in response to infection with *Ascaris* (Kennedy *et al.* 1986). It is entirely possible that future data will provide firmer support for the idea, but at present it seems premature to abandon other lines of enquiry.

One possibility is a role for the MHC in the promotion of disassortative mating, and hence in the avoidance of inbreeding, by a mechanism at least initially analogous to self-incompatibility in plants. Evidence for such a process has come from the tunicate *Botryllus*, in which both colony fusion and gamete fusion are controlled by an MHC-like gene system (Scofield *et al.* 1982). For colony fusion to occur, a single allele at a fusibility locus must be held in common, whereas for successful fertilization the fusibility allele in the sperm must not be identical with either in the parent of the egg; selfing is thus precluded. The system is relaxed if successful fertilization has not occurred within a certain time of egg-production, and the resulting selfed progeny show marked inbreeding depression.

It is not clear if or how a self-incompatibility system based on gametic recognition in external fertilizers could evolve into one based on mate recognition in internal fertilizers, although the prior existence of gametic incompatibility would constitute a selection pressure for the avoidance of mates producing incompatible gametes. If the system responsible for gametic incompatibility in lower chordates is an MHC homologue, it may have undergone this transition, because there is some evidence in mammals of an effect of MHC on mating preferences. There is at present no evidence in mammals for gametic incompatibility associated with the MHC, but there is some evidence for reproductive problems in pairings between individuals holding MHC alleles in common.

It has been suggested that an immunological challenge of mother by foetus, based on MHC dissimilarity, is necessary to prevent a later attack by maternal cells (Beer *et al.* 1981). High rates of spontaneous abortion of chromosomally normal foetuses have been found in human couples who are more alike at Class I HLA loci (reviewed in Beer *et al.* 1981), and when three such women were treated when pregnant with a mixture of foreign lymphocytes, each successfully brought a pregnancy to term (Taylor & Faulk 1981). These results should be regarded with some caution, because there was no control for overall genetic similarity between spouses and between mother and foetus, so the MHC was not necessarily causal in producing the effects. This control was present in a longitudinal study of fertility in Hutterites (Ober *et al.* 1983). The interval between births was higher for couples with more than one HLA-*A* or -*B* allele in common, and a previous study showed no significant effect of inbreeding on this variable. The form of reproductive failure responsible was not investigated. There is also evidence that antigenic dissimilarity between mother and foetus leads to larger placentae in mice (Billington 1964; James 1965), although the effect of placental size on fertility was not investigated in these studies. Between them these data lend some support to the idea that MHC-dissimilarity between mother and foetus, and hence between mates, leads to an enhanced likelihood of successful pregnancy and hence to a higher fertility (but see Clarke & Hetherington (1972)). For this reason, if for no other, there may be selection for disassortative mating with respect to MHC in mammals, and the avoidance of inbreeding could constitute an additional advantage.

There is strong evidence that the MHC influences mouse mating preferences, and that it does so through an effect on odour. The first indication of a role in mate choice came from a series of experiments using congenic strains, differing only at single MHC Class I locus, as a result of backcrossing MHC mutant genotypes into established inbred strains. In mating tests using an oestrus female and two males, one of the same and the other of the congenic strain, mating was in general non-random, usually (on a very small sample of paired strains) with an excess of matings between mice of unlike MHC genotype (Yamazaki *et al.* 1976*a*). Subsequent studies showed that this behaviour persisted when F2 segregants from crosses between the strains were used, ruling out most effects of environmental differences between strains (Yamazaki *et al.* 1978). The incidence of preimplantation pregnancy block by a strange male (Yamazaki *et al.* 1983*a*, 1986) was higher when the new male differed in MHC genotype from the mate, and the scent of urine alone was sufficient to produce the effect. Mice have been successfully trained to discriminate in Y-mazes between the scents of mice differing only at MHC Class I loci (Yamazaki *et al.* 1976*b*, 1983*b*). Similar discrimination of urine has been shown in the rat (Singh *et al.* 1987), and this study also demonstrated the presence of MHC Class I antigen derivatives in the blood and urine. The authors suggested that selective association between different MHC products and other small volatile molecules might be responsible for selective transport into urine, and hence the difference in odour, because rats are unable to discriminate between serum from rats of different MHC haplotype.

It is therefore clear that rats and mice can make olfactory discriminations between conspecifics differing in MHC haplotype, and that these differences can play a role in mate choice and preimplantation abortion. What are far less clear are the population genetic and evolutionary implications of these findings. Although the earlier mouse studies have been repeatedly cited as demonstrating negative assortment (see, for example, Blaustein *et al.* 1987), the data did not approach statistical significance. Ultimately we require to know if polymorphism at the MHC is involved in producing disassortative mating in the field. Two obvious questions are raised by the laboratory studies of mate choice. First, how do the MHC and the adjacent T-complex interact to affect mating preferences? The presence of t alleles has been shown to affect the odour preferences of female mice for males, irrespective of MHC haplotype of the male, and in the field the T-complex and MHC show marked linkage disequilibrium (Egid & Lenington 1985; Lenington & Egid 1985). Second, how do laboratory mate-choice tests relate to events in the field? For instance, several of the above studies showed effects of rearing conditions on mate preferences. In addition, females generally choose males rather than *vice versa* (Partridge & Halliday 1984), whereas the laboratory tests have usually offered only males a choice, although admittedly the outcome may be determined in part by female behaviour. Studies investigating mate choice using animals of known MHC genotype under controlled semi-natural conditions are required. Data from wild populations on mating patterns in respect of MHC are also needed. Any tendency to negative assortment could be a consequence of an effect of the MHC itself, or a reflection of inbreeding avoidance by some other mechanism, and behavioural studies would be necessary to unravel the causal basis.

EVOLUTIONARY SIGNIFICANCE OF THE RME

We have seen that problems of observer bias, lack of repeatability, faulty experimental design and inappropriate analysis probably mean that the RME is considerably less common, even in laboratory experiments, than a casual reading of the literature would suggest. Moreover, it seems unlikely that the mechanisms producing the RME in the laboratory would commonly operate in the field. Many of the laboratory reports involve strains or mutants that do not exist in nature or, if they do, that do not encounter one another. This is true even for the field data from the two-spot ladybird, which involved a comparison of different geographical populations; the available laboratory data suggest that only a one-sided effect is found within single populations. The most likely explanations for the RME are a mixture of fixed, non-assorting females preferences or, probably less commonly, varying male competitive tactics. In the field there is at present only very limited evidence for variable female preferences, and only cases where males differ considerably in mating tactics seem likely to generate two-sided frequency dependence within populations.

The RME is unlikely to be important in maintaining the high levels of genetic polymorphism found in nature. One reason is that female mating preferences would be required to encompass the phenotypic effects of all polymorphic loci. In addition, the preferences in respect to these loci would be required to vary in direction to produce the two-sided frequency-dependence necessary to maintain polymorphism. Varying male competitive tactics may occasionally have this effect. The RME is unlikely to be involved in the avoidance of inbreeding, because it does not necessarily involve assortment, nor does it do so in the majority of cases. Disassortative mating in respect of self-incompatibility alleles in plants, and possibly MHC alleles in chordates, produces an RME, the avoidance of inbreeding and genetic polymorphism. However, these highly specialized cases are not typical. The RME is therefore likely to be of extremely limited evolutionary significance.

REFERENCES

Anderson, M. H., Cornish, E. C., Maus, L., Williams, E. G., Hoggart, R., Atkinson, A., Bonig, I., Grego, B., Simpson, R., Roche, P. J., Haley, J. D., Pehschow, J. D., Niall, H. D., Tregear, G. W., Coghlan, J. P., Crawford, R. J. & Clarke, A. E. 1986 Cloning of cDNA for a stylar gylcoprotein associated with expression of self-incompatibility in *Nicotiniana alata*. *Nature, Lond.* **321**, 38–44.

Anderson, W. W., Levine, L., Olvera, O., Powell, J. R., de la Rosa, M. E., Salceda, V. M., Gaso, M. I. & Guzman, J. 1979 Evidence for selection by male mating success in natural populations of *Drosophila pseudoobscura*. *Proc. natn. Acad. Sci. U.S.A.* **76**, 1519–1523.

Anderson, W. W. & McGuire, P. R. 1978 Mating pattern and mating success of *Drosophila pseudoobscura* karyotypes in large experimental populations. *Evolution* **32**, 416–423.

Andersson, M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature, Lond.* **299**, 818–820.

Antony, C. & Jallon, J.-M. 1982 The chemical basis for sex recognition in *Drosophila melanogaster*. *J. Insect Physiol.* **28**, 873–880.

Averhoff, W. W. & Richardson, R. H. 1974 Pheromonal control of mating patterns in *Drosophila melanogaster*. *Behav. Genet.* **4**, 207–225.

Averhoff, W. W. & Richardson, R. H. 1976 Multiple pheromone system controlling mating in *Drosophila melanogaster*. *Proc. natn. Acad. Sci. U.S.A.* **73**, 591–593.

Banks, M. J. & Thompson, D. J. 1985 Lifetime mating success in the damselfly *Coenagrion puella*. *Anim. Behav.* **33**, 1175–1183.

Bateson, P. (ed.) 1983 *Mate choice*. Cambridge University Press.

Beer, A. E., Gagnon, M. & Quebbeman, J. F. 1981 Immunologically induced reproductive disorders. In *Endocrinology of human infertility: new aspects* (ed. P. G. Crosignani & B. L. Rubin), pp. 419–439. London: Academic Press.

Billington, W. D. 1964 Influence of immunological dissimilarity of mother and foetus on size of placenta in mice. *Nature, Lond.* **202**, 317–318.

Blaustein, A. R., Bekoff, M. & Daniels, T. J. 1987 Kin recognition in vertebrates (excluding primates): empirical evidence. In *Kin recognition in animals* (ed. D. J. C. Fletcher & C. D. Michener), pp. 333–357. Chichester: Wiley.

Bodmer, W. F. 1980 Models and mechanisms for HLA and disease associations. *J. exp. Med.* (*Suppl.*) **152**, 353–357.

Bodmer, W. F. 1984 The HLA system, 1984. In *Histocompatibility testing* (ed. E. D. Albert, M. P. Baur & W. R. Mayr), pp. 11–22. Berlin: Springer-Verlag.

Bodmer, W. F., Trowsdale, J., Young, J. & Bodmer, Julia 1986 Gene clusters and the evolution of the major histocompatibility system. *Phil. Trans. R. Soc. Lond.* B **312**, 303–315.

Borgia, G. 1985 Bower quality, number of decorations and mating success of male satin bower birds (*Ptilonorhynchus violaceus*): an experimental analysis. *Anim. Behav.* **33**, 266–271.

Brakefield, P. 1984 Selection along clines in the ladybird *Adalia bipunctata* in the Netherlands. II. A general mating advantage of melanics and its consequences. *Heredity* **53**, 37–49.

Bryant, E. H. 1979 Inbreeding and heterogametic mating: an alternative to Averhoff and Richardson. *Behav. Genet.* **9**, 249–256.

Bundgaard, J. & Christiansen, F. B. 1972 Dynamics of polymorphisms. I. Selection components in an experimental population of *Drosophila melanogaster*. *Genetics* **71**, 439–460.

Buss, L. W. 1982 Somatic cell parasitism and the evolution of somatic tissue compatibility. *Proc. natn. Acad. Sci. U.S.A.* **79**, 5337–5341.

Buss, L. W. & Green, D. R. 1985 Histocompatibility in vertebrates: the relict hypothesis. *Devl comp. Immun.* **9**, 191–201.

Cade, W. H. 1979 The evolution of alternative male reproductive strategies in field crickets. In *Sexual selection and reproductive competition in insects* (ed. M. Blum & N. A. Blum), pp. 343–379. London: Academic Press.

Cade, W. H. 1981 Alternative male strategies: genetic differences in crickets. *Science, Wash.* **212**, 563–564.

Cade, W. H. & Wyatt, D. R. 1984 Factors affecting calling behaviour in field crickets, *Teleogryllus* and *Gryllus* (age, weight, density and parasites). *Behaviour* **88**, 61–75.

Catchpole, C. K., Dittami, J. & Leisler, B. 1984 Differential response to male song repertoires in female songbirds implanted with oestradiol. *Nature, Lond.* **312**, 563–564.

Charlesworth, D. 1979 Some properties of populations with multilocus homomorphic gametophytic incompatiblity systems. *Heredity* **43**, 19–25.

Charlesworth, D. & Charlesworth, B. 1979*a* The evolutionary genetics of sexual systems in flowering plants. *Proc. R. Soc. Lond.* B **205**, 513–530.

Charlesworth, D. & Charlesworth, B. 1979*b* The evolution and breakdown of S-allele systems. *Heredity* **43**, 41–55.

Clarke, A. G. & Hetherington, M. 1972 Immunogenetic aspects of maternal foetal relations. *J. Reprod. Fert.* (suppl.) **15**, 99–118.

Clutton-Brock, T. H., Guiness, F. E. & Albon, S. D. 1982 *Red deer. Behaviour and ecology of two sexes.* Edinburgh University Press.

Connolly, K., Burnet, B., Kearney, M. & Eastwood, L. 1974 Mating speed and courtship behaviour of inbred strains of *Drosophila melanogaster*. *Behaviour* **48**, 61–74.

Crozier, R. H. 1986 Genetic clonal recognition abilities in marine invertebrates must be maintained by selection for something else. *Evolution* **40**, 1100–1101.

Dal Molin, C. 1979 An external scent as the basis for a rare-male mating advantage in *Drosophila melanogaster*. *Am. Nat.* **109**, 951–954.

Egid, K. & Lenington, S. 1985 Response of male mice to odors of females: effects of T- and H-2-locus genotype. *Behav. Genet.* **15**, 287–295.

Ehrman, L. 1966 Mating success and genotypic frequency in *Drosophila*. *Anim. Behav.* **14**, 332–339.

Ehrman, L. 1969 The sensory basis of mate selection in *Drosophila*. *Evolution* **23**, 59–64.

Ehrman, L. 1970 Simulation of the mating advantage of rare *Drosophila* males. *Science, Wash.* **167**, 905–906.

Ehrman, L., Anderson, W. W. & Blatte, L. 1977 A test for rare male mating advantage at an 'enzyme locus' in *Drosophila*. *Behav. Genet.* **7**, 427–432.

Ehrman, L. & Petit, C. 1968 Genotype frequency and mating success in the *willistoni* species group of *Drosophila*. *Evolution* **22**, 649–658.

Ehrman, L. & Spiess, E. B. 1969 Rare-type mating advantage in *Drosophila*. *Am. Nat.* **103**, 675–680.

Endler, J. A. 1983 Natural selection and sexual selection on color patterns in poeciliid fishes. *Environ. Biol. Fishes* **9**, 173–190.

Ewing, A. W. 1964 The influence of wing area on the courtship of *Drosophila melanogaster*. *Anim. Behav.* **12**, 316–320.

Ewing, A. W. 1983 Functional aspects of *Drosophila* courtship. *Biol. Rev.* **58**, 275–292.

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.

Fontdevila, A. & Mendez, J. 1979 Frequency-dependent mating in a modified allozyme locus of *Drosophila pseudoobscura*. *Evolution* **33**, 634–640.

Grant, B., Burton, S., Contoreggi, C. & Rothstein, M. 1980 Outbreeding via frequency-dependent mate selection in the parasitoid wasp *Nasonia* (= *Mormoniella*) *vitripennis* Walker. *Evolution* **34**, 983–992.

Grant, B., Snyder, G. A. & Glessner, F. 1974 Frequency-dependent mate selection in *Mormoniella vitripennis*. *Evolution* **28**, 259–264.

Grosberg, R. K. & Quinn, J. F. 1986 The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature, Lond.* **322**, 456–459.

Gross, M. R. 1985 Disruptive selection for alternative life histories in salmon. *Nature, Lond.* **313**, 47–48.

Hedrick, P. W. & Thomson, G. 1983 Evidence for balancing selection at HLA. *Genetics* **104**, 449–456.

Hildemann, W. H., Raison, R. L., Cheung, G., Hull, C. J., Akaka, L. & Okamoto, J. 1977 Immunological specificity and memory in a scleractinian coral. *Nature, Lond.* **270**, 219–223.

Hildemann, W. H., Johnston, I. S. & Jokiel, P. L. 1979 Immunocompetence in the lowest metazoan phylum: transplantation immunity in sponges. *Science, Wash.* **204**, 420–422.

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

Howard, R. D. 1978 The evolution of mating strategies in bullfrogs, *Rana catesbiana*. *Evolution* **32**, 850–871.

Jallon, J.-M. 1984 A few chemical words exchanged by *Drosophila* during courtship and mating. *Behav. Genet.* **14**, 441–478.

James, D. A. 1965 Effects of antigenic dissimilarity between mother and foetus on placental size in mice. *Nature, Lond.* **205**, 613–614.

Kence, A. 1981 The rare-male advantage in *Drosophila*: a possible source of bias in experimental design. *Am. Nat.* **117**, 1027–1028.

Kence, A. 1986 Spurious frequency-dependent fitness in *Drosophila*: an artefact caused by marking procedures. *Am. Nat.* **127**, 716–720.

Kence, A. & Bryant, E. H. 1978 A model of mating behavior in flies. *Am. Nat.* **112**, 1047–1062.

Kennedy, M. W., Gordon, A. M. S., Tomlinson, L. A. & Qureshi, F. 1986 Genetic (major histocompatibility complex?) control of the antibody repertoire to the secreted antigens of *Ascaris*. *Parasite Immun.* **9**, 269–273.

Klein, J. 1986 *Natural history of the major histocompatibility complex*. New York: John Wiley and Sons.

Klitz, W., Thomson, G. & Baur, M. P. 1984 The nature of selection at the HLA region based on population data from the ninth workshop. In *Histocompatibility testing* (ed. E. D. Albert, M. P. Baur & W. R. Mayr), pp. 330–332. Berlin: Springer-Verlag.

Klobutcher, L. A. 1977 Ageing and frequency-dependent mating in *Drosophila*. *Behav. Genet.* **7**, 33–36.

Knoppien, P. 1984 The rare male mating advantage: an artifact caused by marking procedures. *Am. Nat.* **123**, 862–866.

Knoppien, P. 1985 Rare male mating advantage: a review. *Biol. Rev.* **60**, 81–117.

Lacy, R. C. 1979 Adaptiveness of rare male mating advantage under heterosis. *Behav. Genet.* **9**, 51–55.

Lenington, S. & Egid, K. 1985 Female discrimination of male odors correlated with male genotype at the *T* locus: a response to *T*-locus or *H*-2-locus variability? *Behav. Genet.* **15**, 53–67.

Lubbock, R. 1980 Clone-specific cellular recognition in a sea anemone. *Proc. natn. Acad. Sci. U.S.A.* **77**, 6667–6669.

Majerus, M., O'Donald, P. & Weir, J. 1982*a* Evidence for preferential mating in *Adalia bipunctata*. *Heredity* **49**, 37–49.

Majerus, M. E. N., O'Donald, P. & Weir, J. 1982*b* Female mating preference is genetic. *Nature, Lond.* **300**, 521–523.

Majerus, M. E. N., O'Donald, P., Kearns, P. W. E. & Ireland, H. 1986 Genetics and evolution of female choice. *Nature, Lond.* **321**, 164–167.

Markow, T. A. 1978 A test for the rare male mating advantage in coisogenic strains of *Drosophila melanogaster*. *Genet. Res.* **32**, 123–127.

Markow, T. A. 1980 Rare male mating advantage among *Drosophila* of the same laboratory strain. *Behav. Genet.* **10**, 553–556.

Markow, T. A., Richmond, R. C., Mueller, L., Sheer, I., Roman, S., Laetz, C. & Lorenz, L. 1980 Testing for rare male advantages among various *Drosophila melanogaster* genotypes. *Genet. Res.* **35**, 59–64.

Maynard Smith, J. 1981 Will a sexual population evolve to an ESS? *Am. Nat.* **117**, 1015–1018.

Maynard Smith, J. 1982 *Evolution and the theory of games*. Cambridge University Press.

Merrell, D. J. 1983 Frequency-dependent mating? *Evolution* **37**, 413–414.

Muggleton, J. 1979 Non-random mating in wild populations of polymorphic *Adalia bipuntata*. *Heredity* **42**, 57–65.

Nasrallah, J. B., Kao, T.-H., Goldberg, M. L. & Nasrallah, M. E. 1985 A cDNA clone encoding an S-locus specific glycoprotein form *Brassica oleracea*. *Nature, Lond.* **318**, 263–267.

Neigel, J. E. & Avise, J. C. 1983 Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: self-recognition analysis and demographic interpretation. *Evolution* **37**, 433–453.

Neigel, J. E. & Avise, J. C. 1985 The precision of histocompatibility response in clonal recognition in tropical marine sponges. *Evolution* **39**, 724–732.

Ober, C. L., Martin, A. O., Simpson, J. L., Hauck, W. W., Amos, D. B., Kostyu, D. D., Fotino, M. & Allen, F. H. 1983 Shared HLA antigens and reproductive performance among Hutterites. *Am. J. hum. Genet.* **35**, 994–1004.

Oberhauser, K. S. 1988 Lack of rare male mating effect using *bw* and *st Drosophila melanogaster* mutants. *Am. Nat.* **131**, 143–148.

O'Donald, P. 1977 Mating advantage of rare males in models of sexual selection. *Nature, Lond.* **267**, 151–154.

O'Donald, P. 1978 Rare male mating advantage. *Nature, Lond.* **272**, 189.

O'Donald, P. 1980 *Genetic models of sexual selection*. Cambridge University Press.

O'Donald, P. 1983 Do female flies choose their mates? A comment. *Am. Nat.* **122**, 413–416.

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

O'Donald, P. & Muggleton, J. 1979 Melanic polymorphism in ladybirds maintained by sexual selection. *Heredity, Lond.* **43**, 143–148.

Partridge, L. 1983 Non-random mating and offspring fitness. In *Mate choice* (ed. P. Bateson), pp. 227–255. Cambridge University Press.

Partridge, L. & Farquhar, M. 1983 Lifetime mating success of male fruitflies (*Drosophila melanogaster*) is related to their size. *Anim. Behav.* **31**, 871–877.

Partridge, L. & Gardner, A. 1983 Failure to replicate the results of an experiment on the rare male effect in *Drosophila melanogaster*. *Am. Nat.* **122**, 422–427.

Partridge, L. & Halliday, T. 1984 Mating patterns and mate choice. In *Behavioural ecology*, 2nd edn, (ed. J. R. Krebs & N. B. Davies), pp. 222–250. Oxford: Blackwell Scientific Publications.

Partridge, L. & Hill, W. G. 1984 Mechanisms for frequency-dependent mating success. *Biol. J. Linn. Soc.* **23**, 113–132.

Partridge, L., Hoffmann, A. & Jones, J. S. 1987 Male size and mating success in *Drosophila melanogaster* and *D. pseudoobscura* under field conditions. *Anim. Behav.* **35**, 468–476.

Petit, C. & Nouaud, D. 1975 Ecological competition and the advantage of the rare type in *Drosophila melanogaster*. *Evolution* **29**, 763–776.

Pot, W., Van Delden, W. & Kruijt, J. P. 1980 Genotypic differences in mating success and the maintenance of the alcohol dehydrogenase polymorphism in *Drosophila melanogaster*. No evidence for overdominance or rare genotype mating advantage. *Behav. Genet.* **10**, 43–58.

Powell, J. R. & Morton, L. 1979 Inbreeding and mating patterns in *Drosophila pseudoobscura*. *Behav. Genet.* **9**, 425–429.

Prout, T. 1971 The relation between fitness components and population prediction in *Drosophila*. I. The estimation of fitness components. *Genetics* **68**, 127–149.

Scofield, V. L., Schlumpberger, J. M., West, L. A. & Weisman, I. L. 1982 Protochordate allorecognition is controlled by a MHC-like gene system. *Nature, Lond.* **295**, 499–502.

Searcy, W. A. 1982 The evolutionary effects of mate selection. *A. Rev. Ecol. Syst.* **13**, 57–85.

Singh, P. B., Brown, R. E. & Roser, B. 1987 MHC antigens in urine as olfactory recognition cues. *Nature, Lond.* **327**, 161–164.

Sinnock, P. 1970 Frequency-dependence and mating behavior in *Tribolium castaneum*. *Am. Nat.* **104**, 469–476.

Spiess, E. B. 1968 Low frequency advantage in mating of *Drosophila pseudoobscura* karyotypes. *Am. Nat.* **102**, 363–379.

Spiess, E. B. 1982*a* Do female flies choose their mates? *Am. Nat.* **119**, 675–693.

Spiess, E. B. 1982*b* Minority mating advantage of certain eye color mutants of *Drosophila melanogaster*. III. Female discrimination and genetic background. *Behav. Genet.* **12**, 209–221.

Spiess, E. B. & Bowbal, D. A. 1987 Minority mating advantage of certain eye color mutants of *Drosophila melanogaster*. IV. Female discrimination among three genotypes. *Behav. Genet.* **17**, 291–306.

Spiess, E. B. & Kruckeberg, J. F. 1980 Minority mating advantage of certain eye color mutants of *Drosophila melanogaster*. II. A behavioral basis. *Am. Nat.* **115**, 307–327.

Spiess, E. B. & Schwer, W. A. 1978 Minority mating advantage of certain eye color mutants of *Drosophila melanogaster*. I. Multiple-choice and single-female tests. *Behav. Genet.* **8**, 155–168.

Spiess, L. D. & Spiess, E. B. 1969 Minority advantage in interpopulational mating of *Drosophila persimilis*. *Am. Nat.* **103**, 155–172.

Stoddart, J. A., Ayre, D. J., Willis, B. & Heyward, A. J. 1985 Self-recognition in sponges and corals? *Evolution* **39**, 461–463.

Tardif, G. N. & Murnick, M. R. 1975 Frequency-dependent selection among wild type strains of *Drosophila melanogaster*. *Behav. Genet.* **5**, 373–379.

Taylor, C. & Faulk, W. P. 1981 Prevention of recurrent abortion with leucocyte transfusion. *Lancet* ii, 68–70.

Tompkins, L. 1984 Genetic analysis of sex appeal in *Drosophila*. *Behav. Genet.* **5**, 411–440.

Van den Berg, M. J., Thomas, G., Hendriks, H. & van Delden, W. 1984 A reexamination of the negative assortative mating phenomenon and its underlying mechanism in *Drosophila melanogaster*. *Behav. Genet.* **14**, 45–61.

Veuille, M. & Mazeau, S. 1986 Variation in sexual behavior and negative assortative mating in *Drosophila melanogaster*. *Behav. Genet.* **16**, 307–317.

White, H. C. & Grant, B. 1977 Olfactory cues as a factor in frequency-dependent mate selection in *Mormoniella vitripennis*. *Evolution* **31**, 829–835.

Wool, D. 1967 Some observations on mating frequencies in *Tribolium castaneum* strains. *Tribolium Information Bulletin* **10**, 182–186.

Wool, D. 1970 Deviations of zygotic frequencies from expectation in eggs of *Tribolium castaneum*. *Genetics* **66**, 115–132.

Yamazaki, K., Beauchamp, G. K., Egorov, I. K., Bard, J., Thomas, L. & Boyse, E. A. 1983*b* Sensory distinction between $H\text{-}2^{b}$ and $H\text{-}2^{bml}$ mutant mice. *Proc. natn. Acad. Sci. U.S.A.* **80**, 5685–5688.

Yamazaki, K., Beauchamp, G. K., Matsuzaki, O., Kupniewski, D., Bard, J. & Thomas, L. 1986 Influence of a genetic difference confined to mutation of H-2K on the incidence of pregnancy block in mice. *Proc. natn. Acad. Sci. U.S.A.* **83**, 740–741.

Yamazaki, K., Beauchamp, G. K., Wyscocki, C. J., Bard, J., Thomas, L. & Boyse, E. A. 1983*a* Recognition of H-2 types in relation to the blocking of pregnancy in mice. *Science, Wash.* **221**, 186–188.

Yamazaki, K., Boyse, E. A., Mike, V., Thaler, H. T., Mathieson, B. J., Abbott, J., Boyse, J., Zayas, Z. A. & Thomas, L. 1976*a* Control of mating preferences in mice by genes in the major histocompatibility complex. *J. exp. Med.* **144**, 1324–1335.

Yamazaki, K., Yamaguchi, M., Andrews, P. W., Peake, B. & Boyse, E. A. 1978 Mating preferences of F2 segregants of crosses between MHC congenic mouse strains. *Immunogenetics* **6**, 253–259.

Yamazaki, K., Yamaguchi, M., Baranoski, L., Bard, J., Boyse, E. A. & Thomas, L. 1976*b* Recognition among mice: evidence from the use of a Y maze differentially scented by congenic mice of different major histocompatibility types. *J. exp. Med.* **150**, 755–760.

Yamazaki, K., Yamaguchi, M., Boyse, E. A. & Thomas, L. 1980 The major histocompatibility complex as a source of odors imparting individuality among mice. In *Chemical signals* (ed. D. Muller-Schwarze & R. M. Silverstein), pp. 267–273. New York: Plenum.