PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Frequency-Dependent Sexual Selection

P. O'Donald and M. E. N. Majerus

Phil. Trans. R. Soc. Lond. B 1988 **319**, 571-586
doi: 10.1098/rstb.1988.0066

Phil. Trans. R. Soc. Lond. B **319**, 571–586 (1988)
Printed in Great Britain

Frequency-dependent sexual selection

By P. O'Donald and M. E. N. Majerus
Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, U.K.

Sexual selection by female choice is expected to give rise to a frequency-dependent sexual advantage in favour of preferred male phenotypes: the rarer the preferred phenotypes, the more often they are chosen as mates. This 'rare-male advantage' can maintain a polymorphism when two or more phenotypes are mated preferentially: each phenotype gains an advantage when it is rarer than the others; no preferred phenotype can then be lost from the population.

Expression of preference may be complete or partial. In models of complete preference, females with a preference always mate preferentially. Models of partial preference are more realistic: in these models, the probability that a female mates preferentially depends on the frequency with which she encounters the males she prefers. Two different 'encounter models' of partial preference have been derived: the O'Donald model and the Charlesworth model. The encounter models contain the complete preference model as a limiting case. In this paper, the Charlesworth model is generalized to allow for female preference of more than one male phenotype. Levels of frequency dependence can then be compared in the O'Donald and Charlesworth models.

The complete preference model and both encounter models are formulated in the same genetical terms of preferences for dominant and recessive male phenotypes. Polymorphic equilibria and conditions for stability are derived for each of the three models. The models are then fitted to data of frequencies of matings observed in experiments with the two-spot ladybird. The complete preference model gives as good a fit as the encounter models to the data of these and other experiments.

The O'Donald and Charlesworth encounter models are shown to produce a very similar frequency-dependent relation. Generally, as females become less choosy, they express their preference with more dependence on male frequency, whereas the resulting selection of the males becomes less frequency dependent. More choosy females are more constant in expressing their preference, producing greater frequency dependence in the selection of the males.

Introduction

When females choose preferentially between different male phenotypes, the preferred males gain a sexual advantage that is almost inevitably frequency-dependent. If an approximately constant proportion of females have a preference for a specific phenotype, relatively more of them will prefer the phenotype when it is rare than when it is common: the rarer the phenotype, the greater its advantage. This negative frequency dependence in sexual advantage arises in all recent models of sexual selection by female choice. On the other hand, male competition for females – Darwin's 'Law of Battle' – does not necessarily give rise to frequency-dependent sexual selection.

Sexual selection by female choice has been described and analysed in terms of three models that make different assumptions about how the females express their preferences (O'Donald 1980*a*): complete, partial and frequency-dependent expression of preference. In models of complete preference, some females, who perhaps may have a genetic preference for a specific phenotype, always mate preferentially; or at least some fixed proportion of them do so. The other females exercise no preference and mate at random. In other words, the preferred male phenotype gives a display that is essential to elicit the mating responses of the females with the preference. These are the simplest models of preferential mating (O'Donald (1962, 1967, 1973); results summarized in O'Donald (1980*a*)). They produce an extreme sexual advantage when the preferred males are very rare: the same proportion of females still mate only with preferred males who thus take part in the same number of matings regardless of their rarity.

In partial preference or 'encounter' models, the chances of encountering a preferred male determine whether a female mates preferentially. Two different models of this sort have been widely used in the study of the effects of sexual selection. O'Donald's encounter model (O'Donald 1978*a*, 1979, 1980*a*) is based on the assumption that females encounter a sequence of courting males in their search for a mate. The males might be holding display territories on a lek which the females then visit, as for example in the ruff, *Philomachus pugnax*. If the females encounter a succession of males not of the phenotype they prefer, then after a number of such disappointments, they give up the search and mate with the next male they meet. The model assumes that females with preferences respond to the stimulation of male courtship at two thresholds: they respond at a lower threshold towards preferred males; but a certain extra number of encounters with non-preferred males will raise their level of stimulation to a higher threshold at which they can respond to any male. The probability of encountering a succession of non-preferred males without encountering a preferred male thus determines the probability of mating preferentially. This is a function of the frequencies of the males. We refer to this model as the 'OD encounter model', or 'OD model'.

Charlesworth & Charlesworth (1975, 1980) put forward an alternative model in which females have constant probabilities of mating with different phenotypes of males. In their original formulation, they assumed that all females mated according to these probabilities; rare males then gain no frequency-dependent advantage. This model describes the matings of males with different competitive advantages equally well. Lande (1981) and Kirkpatrick (1982) used variations of this basic model to describe the matings of females with genetic preferences for specific males. In Lande's polygenic model of sexual selection for a quantitative character, a female with a particular preference value has probabilities of mating that depend on the preference value of the female and the character values and frequencies of the males. In Kirkpatrick's haploid model of the evolution of a preference gene, all females with the preference gene have a fixed probability of mating with the preferred males; the frequencies of the matings are proportional to the product of female mating probability and male frequency. Only some of the females carry the preference gene and mate preferentially, so the resulting selection is frequency dependent. In this paper, the Charlesworth–Lande–Kirkpatrick model, which we call the 'CCLK encounter model', or 'CCLK model', is generalized so that different proportions of females express preferences for different male phenotypes. We can thus compare the OD and CCLK models for goodness-of-fit to existing data and the levels of frequency-dependent male advantage they produce.

In the encounter models, the proportion of females that mate preferentially is determined by the chance they meet a preferred male. O'Donald (1980*a*) analysed other models of frequency-dependent expression of preference in which the initial encounter with a courting male determined whether a preference was then expressed. This concept was based on a suggestion of Spiess & Ehrman (1978) that females would avoid the phenotype of male first encountered and so mate with others unlike it. Thus if females had a genetic preference for a specific phenotype, they would only mate preferentially if the first male they encountered was not of the preferred phenotype: the first encounter thus determined whether the preference was expressed or not. Such a model in which females avoid the first male encountered gives rise to negative frequency dependence in the expression of the preference as well as a negative frequency dependence in the advantage the males consequently gain. O'Donald (1980*a*) analysed the genetic consequences of this model and a corresponding model with positive frequency-dependent expression of preference. Formally, the latter model is similar to the CCLK model. In both these models, preferences for specific phenotypes show frequency-dependent expression. Spiess & Ehrman (1978) had originally assumed, however, that females might avoid any male first encountered and thus acquire a preference for any other male: they did not assume that only specific phenotypes might be the object of the preference. Any rare male would thus acquire a preference as a result of this general 'avoidance model' of female mating behaviour. As O'Donald (1978*b*) pointed out, this would seem to be maladaptive behaviour, for it would produce matings in favour of rare, deleterious males. It is difficult to understand how genes for this expression of preference could possibly evolve.

All the models we have outlined produce a frequency-dependent mating advantage of the preferred males. The frequency dependence is negative except in some special cases (an example is given in §2.2), for given that only a certain proportion of the females express a particular preference, it follows that when preferred males are rare they must each take part in more of the preferential matings, giving an advantage to being rare. The term 'rare-male advantage' has been widely used to describe any negative frequency dependence in male sexual advantage (Ehrman 1970; Ehrman & Spiess 1969; Knoppien 1985; Spiess & Spiess 1969). It was first observed in matings of mutant and wild-type *Drosophila* (Petit 1954). In these and many other examples, however, it was not clear that female choice determined the advantage gained. Partridge (1983) quoted A. W. Ewing's finding (from his Ph.D. thesis) that a rare-male advantage might be generated by male competition when truncation selection is applied in a population with two male phenotypes differing in mating ability. Partridge & Hill (1984) review several other models incorporating variation in male mating ability. Whether any of these models would produce the high levels of frequency dependence observed in some of Ehrman & Spiess's experiments is doubtful: goodness-of-fit appears not to have been tested. Partridge (1983) also criticises Ehrman & Spiess's theory that the expression of female preference is itself frequency-dependent. She points out that no direct evidence for female choice has been found in *Drosophila*. The fact that rare males may gain a mating advantage is now widely accepted, however: in a general review, Knoppien (1985) finds several convincing examples in *Drosophila* and other species.

Part of the current debate about the rare-male advantage appears to stem from semantic confusion: is it the preference or the mating advantage that is frequency dependent? Ehrman & Spiess have argued that the expression of female preference will be frequency-dependent: in their avoidance model, any rare male phenotype then gains an advantage. For example, if there are two male phenotypes, the rare-male advantage will be 'two-sided', the preference for each phenotype increasing as it becomes rarer. But, as we have seen, it is not necessary for the expression of preference to be frequency-dependent to produce this rare-male advantage. A genetic preference expressed in almost any way will give a frequency-dependent sexual advantage to the preferred males. If more than one phenotype is the object of constant preference, a two-sided advantage is then produced: O'Donald (1983*a*) showed that this model could produce exactly the same probabilities as Ehrman & Spiess's avoidance model. If only one phenotype is preferred, the advantage is then 'one-sided': one phenotype always has an advantage over the others, but the advantage is greater at lower frequencies. We have followed Knoppien in applying the term 'rare-male advantage' to any case in which sexual advantage increases with increasing rarity. We apply the term not to a particular mode of expression of preference, but to the general form of sexual advantage gained by one or more of the male phenotypes.

MODELS OF PREFERENTIAL MATING

The complete preference model

O'Donald (1980*a*) analysed many different genetical models that incorporate the concept of complete expression of preference. Results have been derived for general multiple allelic systems with a series of both dominant and co-dominant alleles (Karlin & O'Donald 1981). Natural selection and assortative mating have also been incorporated in the models (O'Donald 1980*a*; O'Donald *et al.* 1984). Here we analyse a simple genetic model with two phenotypes, one dominant to the other. The other preference models – the encounter models – will also be analysed assuming the same genetical system. This has the advantage that sexual selection of two phenotypes has been observed in many species. The complete preference model and the corresponding encounter models can easily be fitted to data of numbers of matings of two phenotypes.

In the complete preference model, we simply assume that the two phenotypes 'A' (genetically AA or Aa and hence dominant) and 'B' (genetically recessive aa) occur at frequencies $1-w$ and w. Proportions α and β of the females prefer to mate with 'A' and 'B' whereas the remaining $1\text{-}\alpha\text{-}\beta$ mate at random with either phenotype. The frequencies of matings with 'A' and 'B' males are thus as follows:

$$\left.\begin{aligned} P_A &= \alpha+(1-w)\,(1-\alpha-\beta),\\ P_B &= \beta+w(1-\alpha-\beta).\end{aligned}\right\} \qquad (1)$$

This formulation implicitly assumes that matings are polygynous, for regardless of how many females prefer them, males still mate with the randomly mating females at their population frequencies $1-w$ and w. Because females do not discriminate between AA and Aa males, the matings with these males will be divided in the ratio $u/(1-w):v/(1-w)$, where u and v are the frequencies of the genotypes AA and Aa $(u+v = 1-w)$. Females express their preferences regardless of what genotype, AA, Aa or aa, they themselves possess: we assume there is no assortment in the expression of preference. Of course, the male preferred character may either be expressed in both sexes or sex-limited to males. Highly developed characters of male display – the plumage of the male ruff or peacock for example – are of course sex-limited, but many sexually selected characters are equally expressed in both sexes. Given these assumptions, we then obtained the following mating frequencies (see O'Donald 1980*a*):

mating	frequency
AA × AA	$\alpha u^2/(1-w)+u^2(1-\alpha-\beta)$
AA × Aa	$2\alpha uv/(1-w)+2uv(1-\alpha-\beta)$

AA × aa	$\alpha uw/(1-w)+\beta u+2uw(1-\alpha-\beta)$
Aa × Aa	$\alpha v^2/(1-w)+v^2(1-\alpha-\beta)$
Aa × aa	$\alpha vw/(1-w)+\beta v+2vw(1-\alpha-\beta)$
aa × aa	$\beta w+w^2(1-\alpha-\beta)$.

The genotypic frequencies in the following generation are then given by the recursion equations

$$u' = \alpha p^2/(1-w)+p^2(1-\alpha-\beta), \tag{2}$$

$$v' = \alpha p(2q-w)/(1-w)+\beta p+2pq(1-\alpha-\beta), \tag{3}$$

and

$$w' = q^2-pq[\alpha w-\beta(1-w)]/(1-w). \tag{4}$$

We then find the gene frequency of A as $p = u+v/2$ in one generation and $p' = u'+v'/2$ in the next generation:

$$p' = p+p[\alpha w-\beta(1-w)]/2(1-w). \tag{5}$$

At equilibrium therefore,

$$\alpha w = \beta(1-w), \tag{6}$$

giving the phenotypic frequency of '*a*' at equilibrium

$$w^* = \beta/(\alpha+\beta). \tag{7}$$

Putting the recursion equation in the form

$$p' = p+p(w-w^*)(\alpha+\beta)/2(1-w), \tag{8}$$

it is easy to show that the polymorphic equilibrium point is globally stable. If $w > w^*$, then $p' > p$ because all terms are positive. The equation for w' then shows that $w' < w$. Similarly, if $w < w^*$, then $p' < p$ and $w' > w$. Hence $w \rightarrow w^*$ for all values of w. The polymorphic equilibrium point $w^* = \beta/(\alpha+\beta)$ is always attained. This stability is derived from the rare male effect: the phenotype with frequency below equilibrium has the selective advantage and therefore increases until the equilibrium is reached. At the equilibrium point the two phenotypes have equal relative fitness.

The OD model

Suppose a female has a preference for 'A' males. She has received sufficient stimulation to mate with an 'A' male if she meets one. But she encounters a succession of 'B' males. If she encounters m 'B' males, she will have been stimulated to a higher threshold at which she can respond to any male, 'A' or 'B'. So she mates with the next male she meets. If w is the frequency of 'B' in the population, the probability that the female does not meet an 'A' male in the m encounters is w^m. $1-w^m$ is therefore the probability that she meets, and hence mates with, an 'A' male in the course of these encounters. This probability, plus the probability that the $(m+1)$th male is an 'A', is the total probability that she mates with an 'A' male, i.e.

$$(1-w^m)+(1-w)\,w^m = 1-w^{m+1}. \tag{9}$$

The overall probabilities of the matings are given by the equations

$$P_A = \alpha(1-w^{m+1})+\beta(1-w)^{n+1}+(1-w)(1-\alpha-\beta) \tag{10}$$

and

$$P_B = \alpha w^{m+1}+\beta[1-(1-w)^{n+1}]+w(1-\alpha-\beta). \tag{11}$$

In this model, the equilibrium frequency of 'B' is given by the solution of the equation

$$\alpha w[1-w^m]-\beta(1-w)[1-(1-w)^n]=0. \tag{12}$$

The equilibrium is stable provided m, $n > 1$. If $m, n = 1$ then the matings with males occur at frequencies

$$P_A = (1-w)[1+w(\alpha-\beta)] \tag{13}$$

and

$$P_B = w[1-(1-w)(\alpha-\beta)]. \tag{14}$$

Here the frequency dependence is positive: no polymorphism can be stable. The recursion in gene frequency is given by (O'Donald 1980*a*):

$$p' = p+pw(\alpha-\beta)/2, \tag{15}$$

showing that either 'A' fixes in the population ($\alpha > \beta$) or 'B' fixes ($\alpha < \beta$). When $m, n > 1$, then the frequency dependence is negative and polymorphisms are maintained. O'Donald (1980*a*) discusses particular cases of the parameter values.

The CCLK model

Males of the phenotype 'A' are mated preferentially by α of the females. Given equal frequencies of the males, these females then mate with 'A' and 'B' males in the ratio $k{:}1{::}$'A':'B'. The assumption here is that $k > 1$ giving a higher probability of mating with the preferred 'A' males. Among these females, preferential matings with 'A' males occur in the population with relative frequency

$$k(1-w)/[k(1-w)+w]. \tag{16}$$

The mating frequency is thus proportional to the relative probability of choosing an 'A' male and the probability of encountering an 'A' male. Similarly, 'B' phenotypes are preferred by β of the females and mate with them with relative frequency

$$hw/[hw+1-w], \tag{17}$$

where the mating probabilities of females who prefer 'B' males are in the ratio $1{:}h{::}$'A':'B'. Hence we obtain the overall probabilities of mating with 'A' and 'B' males:

$$P_A = \alpha k(1-w)/[k(1-w)+w]+\beta(1-w)/[hw+1-w]+(1-w)(1-\alpha-\beta) \tag{18}$$

and

$$P_B = \alpha w/[k(1-w)+w]+\beta hw/[hw+1-w]+w(1-\alpha-\beta). \tag{19}$$

This formulation represents an extension of the Charlesworth & Kirkpatrick model in which females prefer only one phenotype ($\alpha = 1$, $\beta = 0$). Our model has preferences for two phenotypes with only a proportion of the females exercising the preferences. The model is thus exactly comparable in structure with O'Donald's complete preference and encounter models. As in the OD encounter model, it has four parameters. When $k, h \rightarrow \infty$, the model becomes the complete preference model. The mating frequencies are easily shown to be as follows:

mating	frequency
AA × AA	$\alpha ku^2/[k(1-w)+w]+\beta u^2/[hw+1-w]+u^2(1-\alpha-\beta)$
AA × Aa	$2\alpha kuv/[k(1-w)+w]+2\beta uv/[hw+1-w]+2uv(1-\alpha-\beta)$
AA × aa	$\alpha uw(k+1)/[k(1-w)+w]+\beta uw(h+1)/[hw+1-w]+2uw(1-\alpha-\beta)$

Aa × Aa	$\alpha k v^2/[k(1-w)+w]+\beta v^2/[hw+1-w]+v^2(1-\alpha-\beta)$
Aa × aa	$\alpha v w(k+1)/[k(1-w)+w]+\beta v w(h+1)/[hw+1-w]+2vw(1-\alpha-\beta)$
aa × aa	$\alpha w^2/[k(1-w)+w]+\beta h w^2/[hw+1-w]+w^2(1-\alpha-\beta)$.

The general recursion equations

$$p' = p+pw\{\alpha(k-1)/[k(1-w)+w]-\beta(h-1)/[hw+1-w]\}/2 \tag{20}$$

and

$$w' = q^2-pqw\{\alpha(k-1)/[k(1-w)+w]-\beta(h-1)/[hw+1-w]\} \tag{21}$$

show that equilibrium is reached at the frequency of 'B' given by

$$w^* = [\beta k(h-1)-\alpha(k-1)]/[(\alpha+\beta)(k-1)(h-1)]. \tag{22}$$

As expected, we see that as $k, h \to \infty$, $w^* \to \beta/(\alpha+\beta)$, which is the equilibrium point in the complete preference model. By a similar argument to that which we used for the complete preference model, it is easy to show that the single polymorphic equilibrium in the CCLK model is also globally stable subject to the conditions $\alpha, \beta > 0$ and $k, h > 0$. These conditions are of course the premises on which the model has been derived and therefore necessarily true. Again, the stability is a consequence of the negative frequency dependence in the sexual advantages of the male phenotypes. As we shall show in fitting the models to data, this frequency dependence, and hence the stability, increases as k and h increase. The model is in fact very similar to the OD model which also shows increasing frequency dependence and stability as m and n increase.

Models of preferential mating in monogamous species

The models described and analysed in the previous sections all assume that matings are polygynous: males can mate several times, both preferentially and randomly with the different groups of females. All males are assumed always to be available for mating; hence the frequencies at which they may be chosen remain the population frequencies of the phenotypes. This is probably a fair assumption when males are available in large groups, at a lek for example, which females visit in succession to be mated. Sexual selection is by no means restricted to males in polygynous species, however. Indeed, one of the most fully investigated examples of sexual selection in a natural population in the field is the sexual selection of the melanic and non-melanic phenotypes of the Arctic skua, *Stercorarius parasiticus*, a seabird of the northern hemisphere that breeds in a range from about 58° N to 80° N (see O'Donald 1980*b*, 1983*b*).

In a monogamous species, an obvious problem is how the males gain a sexual advantage; for if all individuals eventually mate, the non-preferred males will eventually find mates even though they may take much longer to do so than the preferred males. The solution to this problem was first given by Darwin (1871). He suggested that females arriving to breed early in the season would both be better nourished and rear more chicks than retarded females arriving late. The early females have the first choice of the males who are assumed to be already on the breeding grounds. The early females can thus mate with the preferred males and the early matings will be more fertile or more successful than the later matings: on average, therefore, the preferential matings will take place earlier and produce more offspring than the matings with non-preferred males. Hence the preferred males will gain a selective advantage.

In the Arctic skua, sexual selection takes place precisely as Darwin postulated: breeding success declines sharply towards the end of the breeding season; when new pairs are being formed, melanic males (which may be intermediate or dark in plumage) consistently obtain mates before the non-melanic pale males (which have white or pale underparts). On average, the melanic males in new pairs breed very significantly earlier than non-melanics and gain a considerable selective advantage from their earlier breeding. Because the breeding ecology of the Arctic skua has been studied in great detail (see O'Donald 1983*b*), the process of sexual selection can be simulated in a computer as it may actually occur in the natural population. As Darwin assumed, the males hold territories on the breeding grounds where the females come and visit them. Having paired and mated, a nest is made and the chicks are reared within the territory. The pair are strictly monogamous; having paired, a male is then removed from the pool of available males that newly arriving females can choose from. O'Donald (1976, 1980*b*, 1983*b*) set up detailed computer models of this behaviour, assuming that a proportion of females exercise a preference for the melanic males, though these females will mate with other males if all melanics are already mated. These models are thus similar to encounter models on a lek: if a preferred male is available on the lek, he will be chosen; if not, mating takes place with any other available male. The models show that exactly the same equilibria will be reached in the monogamous Arctic skua as in polygynous species. The frequency dependence is not necessarily negative, however. At certain parameter values, fitness may be roughly constant or even show some positive frequency dependence; stable polymorphisms cannot then be maintained. O'Donald (1980*a*, 1983*b*) also analysed simplified models of monogamous sexual selection in which preferential matings are assumed to take place at a higher average fertility than random matings. The details of the Arctic skua's ecology are thus eliminated from these models; they still normally lead to the same equilibria as found in the polygynous models. As usual, stability depends on negative frequency dependence.

O'Donald (1976, 1980*b*, 1983*b*) used his computer models to estimate the Arctic skua's mating preferences: the models were fitted to the data of the breeding dates of the melanic and non-melanic phenotypes among new pairs. The excellent fit of the models, with the absence of any effect of male competition on breeding date, strongly supports the hypothesis of sexual selection by female choice in the Arctic skua. The details of sexual selection in the Arctic skua have been fully described in O'Donald (1983*b*) and will not be further discussed in this paper.

FITTING THE MODELS TO DATA

The two-spot ladybird

The data we shall fit to the models have all been obtained from our own studies of sexual selection in the ladybird. Some of the data is original, not previously having been published or analysed. Some populations of the two-spot ladybird show a mating advantage of the melanic (black with red spots) males: melanic males are found in mating pairs at higher frequency than in the population (Majerus *et al.* 1982*a*; O'Donald *et al.* 1984). Experiments on matings in population cages, mating boxes and petri-dishes have all produced estimates of preference consistent with those obtained from matings in the natural populations. Selection experiments have shown that the mating preference for melanic males is highly heritable and can be raised to levels at which a majority of the females are mating preferentially (Majerus *et al.* 1982*b*;

O'Donald & Majerus 1985). Isofemale lines have been selected in which females are apparently homozygous for a single preference gene (Majerus *et al.* 1986).

To test the goodness-of-fit of the preference models, matings should be observed at different fixed frequencies of the phenotypes. The models must fit the observed level of frequency dependence in the data. In an early experiment, Majerus *et al.* (1982*a*) observed matings among two phenotypes *quadrimaculata* (Q) and *typica* (T) placed at fixed frequencies in a population cage. Q is the four-spot melanic (black with four red spots); T is the two-spot non-melanic (red with two black spots). The sample was originally obtained from a large population of ladybirds at Keele, U.K., where melanics form about 30% of the population. After mating, males were replaced in the cage to avoid the statistical problem of sampling without replacement. The data are shown in table 1 (*a*). A similar experiment was carried out using a sample of ladybirds collected in Glasgow, U.K., where melanics form about 60% of the population. The data of matings in the Glasgow sample are shown in table 1 (*b*).

TABLE 1. MATING TESTS ON QUADRIMACULATA (Q) AND TYPICA (T) PHENOTYPES OF THE TWO-SPOT LADYBIRD IN POPULATION CAGES AT THREE DIFFERENT PHENOTYPIC RATIOS

(In each of these tests, 200 ladybirds were used. (G1) indicates that the ladybirds were the first generation produced from a sample collected in the field. (field) indicates that the ladybirds were the original field sample. 'Mating advantage' gives the number of matings of Q males relative to their frequency. The Glasgow sample shows clear frequency dependence as expected, but the Keele sample shows the greatest advantage at the ratio 5Q:5T. However, the estimated mating advantage has a high standard error. The mating preference model (which entails frequency dependence) is justified by the known genetic preference and gives just as good a fit to the Keele sample as a model with constant fitnesses.)

	numbers of matings (males shown 1st)				
ratio in cage	Q×Q	Q×T	T×Q	T×T	mating advantage
	(*a*) tests on ladybirds sampled at Keele				
3Q:7T (G1)	29	48	26	61	2.06
5Q:5T (G1)	42	33	16	16	2.34
7Q:3T (G1)	131	51	27	15	1.86
	(*b*) tests on ladybirds sampled at Glasgow				
3Q:7T (field)	20	28	17	26	2.60
3Q:7T (G1)	16	29	19	29	2.19
5Q:5T (G1)	36	32	17	15	2.12
7Q:3T (G1)	44	39	9	12	1.69

The models were fitted to the data by maximum likelihood by using a trial-and-error method to find the maximum-likelihood (ML) estimates of the parameters of the models. In this method the parameters are varied at random until a higher likelihood is found; the magnitude of the random variation is progressively reduced until the maximum likelihood has finally been attained. In fitting the models to the ladybird data, no preference is estimated for the non-melanic T phenotype. This is corroborated by the results of selection experiments: selection rapidly increased the preference for Q; selection of females that mated with T males rapidly eliminates the preference for Q but produces no preference for T. The females have a genetic preference for Q but not for T.

(*a*) *Keele data*

Before fitting any model of preferential mating, a simple model of random mating gives a value of χ^2 for goodness-of-fit of $\chi^2_9 = 58.9059$.

With nine degrees of freedom, this is highly significant. The models give the following estimates of parameters and χ^2 values after fitting.

complete preference	OD model	CCLK model
$\hat{\alpha} = 0.305$	$\hat{\alpha} = 0.398$	$\hat{\alpha} = 0.710$
	$\hat{m} = 3$	$\hat{k} = 2.86$
$\chi^2_8 = 7.0408$	$\chi^2_7 = 4.7101$	$\chi^2_7 = 4.8378$

Clearly, the complete preference model is a sufficiently close fit, leaving a non-significant residual χ^2 after fitting. The OD and CCLK models do improve the fit, but not significantly; for the value of the residual χ^2 is only reduced by 2.33.

(*b*) *Glasgow data*

Before fitting the preferential mating models, simple random mating gives $\chi^2_{12} = 82.8227$. After fitting we have the following estimates.

complete preference	OD model	CCLK model
$\hat{\alpha} = 0.311$	$\hat{\alpha} = 0.354$	$\hat{\alpha} = 0.418$
	$\hat{m} = 5$	$\hat{k} = 9.11$
$\chi^2_{11} = 27.6348$	$\chi^2_{10} = 27.5947$	$\chi^2_{10} = 27.6590$

No model provides any better fit than the others. A residual heterogeneity remains after fitting, as shown by the significant value $\chi^2_{11} = 27.63$ for the complete preference model. Detailed analysis of the data shows that this heterogeneity is entirely accounted for by the experiment at the ratio 7Q:3T. In this experiment a greater proportion of T females mated than the ratio predicts. In fact, among females at the ratio 7Q:3T in the population cage, the ratio of mating females was 53Q:51T. This gives the highly significant value $\chi^2_1 = 17.9505$, which thus accounts for most of the residual heterogeneity in the data. In the other experiments, the females mated at the ratio of phenotypes as placed in the cage, showing no significant selection of females. In the experiment at 7Q:3T, females were taken from a subsequent generation produced after the original sample had been collected in Glasgow. It is possible that these females may have been at different ages after emergence. For example, if many of the Q females had recently emerged, then they would certainly have been less ready to mate than the others. This is just a speculative explanation of what might produce a significant difference in the female mating ratio. It would not be expected to affect the preferential mating for males which is consistent regardless of whether virgin or experienced females are used in the mating tests.

The fitting of the models shows that the preference in the Glasgow sample is higher, with greater frequency dependence in the matings: the values of the parameters m and k are estimated to be greater in the Glasgow population, showing that preference is more completely expressed. But it should be stressed that the complete preference model is an adequate fit to both Keele and Glasgow data.

Data of Mormoniella vitripennis

Mormoniella vitripennis is a parasitic wasp for which various eye and body colour mutants have been found. Grant *et al.* (1974) obtained data on the matings of mutant and wild-type phenotypes in a carefully controlled experiment. Females were used at equal frequencies, mutant (m) to wild-type (+), but males were offered at the ratios 2(+):8(m), 5(+):5(m) and 8(+):2(m). A frequency-dependent model can therefore be fitted to the data of the matings. The matings show assortment both of wild-type with wild-type and mutant with mutant. O'Donald (1980*a*) fitted a model that combined preferential mating without assortment with assortative mating for both phenotypes. This combined model (Karlin & O'Donald 1978) gave an excellent fit to the data. (For details of the model and the procedure of fitting, see O'Donald (1980*a*).)

The data of Grant *et al.* (1974) are shown in table 2. As for the ladybird data, we have fitted the complete preference and encounter models to the data. The added complication of assortment has not been incorporated into the encounter models: to do so would entail adding four additional parameters to the four parameters already present: assortative mating parameters corresponding to the parameters α, β, k and h. Before fitting the models, we find $\chi^2_9 = 96.6433$. After fitting, we find the following estimates and χ^2 values.

TABLE 2. MATING TESTS ON THE PARASITIC WASP *MORMONIELLA VITRIPENNIS*

(For the details of these experiments, see Grant *et al.* (1974).)

	numbers of matings (♂ shown 1st)			
ratio in cage	(+) × (+)	(+) × (m)	(m) × (+)	(m) × (m)
2(+):8(m)	64	38	78	126
5(+):5(m)	101	63	43	92
8(+):2(m)	131	100	35	47

complete preference	OD model	CCLK model
$\hat{\alpha} = 0.203$	$\hat{\alpha} = 0.233$	$\hat{\alpha} = 0.372$
$\hat{\beta} = 0.124$	$\hat{\beta} = 0.136$	$\hat{\beta} = 0.248$
	$\hat{m} = 9$	$\hat{k} = 8.36$
	$\hat{n} = 49$	$\hat{h} = 9.45$
$\chi^2_7 = 50.359$	$\chi^2_5 = 50.376$	$\chi^2_5 = 50.428$

Clearly, without the assortative mating, none of these models fit the data any better than the others. The highly significant residual heterogeneity disappears when the assortative mating is incorporated (O'Donald 1980*a*). The high values of the parameters, m and n, k and h, show that the complete preference model is sufficient to give the observed level of frequency dependence in the data. These parameters determine the proportion of females that express their preferences depending on the frequency of encounter with the preferred males. In the following section, we show how the parameters of the models determine the levels of frequency dependence in the sexual advantage of the males.

FREQUENCY DEPENDENCE IN MODELS OF PREFERENTIAL MATING

As we have seen, models of preferential mating inevitably give rise to frequency dependence in the males' sexual advantage: generally, rare males gain the advantage; thus we observe a 'rare-male effect'. In the encounter models, which aim to give a realistic description of mate choice, the proportion of females that express their preference becomes frequency dependent because it depends on the probability of encountering the preferred males. Models have also been analysed in which expression of preference is intrinsically frequency dependent in the sense that the first encounter with a courting male determines whether a female will express a preference in subsequent matings or what preference she will express (O'Donald 1980*a*; Spiess & Ehrman 1978; Spiess 1983). These models produce similar formulations to the encounter models.

In the OD model, the frequency of the matings of the 'A' males relative to their frequency in the population is given by

$$P_{\mathrm{A}}/(1-w) = \alpha(1-w^{m+1})/(1-w)+\beta(1-w)^{n}+1-\alpha-\beta = f_{\mathrm{A}}, \tag{23}$$

where f_{A} is the relative fitness of the 'A' phenotype compared with the 'B' phenotype. At $w = 1$,

$$f_{\mathrm{A}} = \alpha(m+1)+1-\alpha-\beta = 1+\alpha m-\beta. \tag{24}$$

At $w = 0$,

$$f_{\mathrm{A}} = 1. \tag{25}$$

As 'A' decreases in frequency from 100 to 0% in the population, we see that the fitness of 'A' increases from 1 to $1+\alpha m-\beta$, an increase of $\alpha m-\beta$. If $m = 1$, this may either be an increase or decrease depending on whether $\alpha > \beta$ or not. When $m = 1$ and $n = 1$, either one or the other phenotype always has the advantage; as shown in §2.2, polymorphisms can never be maintained. At values $m, n > 1$, frequency dependence is always negative over at least part of the frequency range; unless the parameter values lead to fixation of one of the phenotypes, stable polymorphisms will then exist.

In the CCLK model, the relative fitness of the 'A' males is given by

$$f_{\mathrm{A}} = \alpha k/[k(1-w)+w]+\beta/[hw+1-w]+1-\alpha-\beta. \tag{26}$$

At $w = 1$,

$$f_{\mathrm{A}} = \alpha k+\beta/h+1-\alpha-\beta \tag{27}$$

and at $w = 0$

$$f_{\mathrm{A}} = 1,$$

showing that as 'A' declines in frequency from 100 to 0%, its fitness changes from 1 to $1+\alpha(k-1)-\beta(h-1)/h$. For equal values of α and β, this is always an increase because, $k, h > 1$, thus showing a rare male effect as in the OD model.

The actual changes in relative fitness can be illustrated using the values of the parameters estimated by the fitting of the models to the ladybird data. In §3.1, we obtained the following estimates from the data of the matings of the Keele and Glasgow samples.

	OD model	CCLK model
Keele	$\hat{\alpha} = 0.389$, $\hat{m} = 3$	$\hat{\alpha} = 0.710$, $\hat{k} = 2.86$
Glasgow	$\hat{\alpha} = 0.354$, $\hat{m} = 5$	$\hat{\alpha} = 0.418$, $\hat{k} = 9.11$

These values give the fitness shown in table 3. A more than 2-fold increase in fitness occurs as the preferred phenotype decreases in frequency from 100 to 0% in the population. All the models give similar fitness values at the frequencies 0.3, 0.5 and 0.7. These were the phenotypic frequencies used in the population cage. The fitnesses we see in the table at these frequencies show the frequency dependence in the observed numbers of matings, for it is essentially to this level of frequency dependence that the models are being fitted. At lower frequencies, the models diverge widely in the fitnesses predicted, suggesting that the models might be discriminated if matings were observed when very low population frequencies of the melanic phenotypes are used in the mating test. It appears to be in the frequency range 0.1–0 that the models are most sensitive to variation in frequency.

TABLE 3. COMPARISON OF FREQUENCY DEPENDENCE IN THE OD AND CCLK MODELS WHEN FITTED TO THE LADYBIRD DATA

frequency of melanics	relative fitness of Q (melanic) and T (non-melanic)							
	Keele data fitted				Glasgow data fitted			
	OD model		CCLK model		OD model		CCLK model	
$1-w$	Q	T	Q	T	Q	T	Q	T
1.0	1.00	0.60	1.00	0.54	1.00	0.65	1.00	0.63
0.7	1.17	0.61	1.17	0.60	1.15	0.65	1.15	0.64
0.5	1.35	0.65	1.34	0.66	1.34	0.66	1.34	0.66
0.3	1.61	0.74	1.59	0.75	1.69	0.71	1.69	0.70
0.2	1.78	0.81	1.77	0.81	1.95	0.76	2.03	0.74
0.1	1.97	0.89	2.00	0.89	2.30	0.86	2.68	0.81
0.05	2.08	0.94	2.15	0.94	2.52	0.92	3.29	0.88
0	2.19	1.00	2.32	1.00	2.77	1.00	4.38	1.00

Because each female is assumed to mate only once at the same average fertility, the mean population fitness does not change: this is entirely determined by the females' fertility which is constant in these models. The male fertilities are equal only at the polymorphic equilibrium. On either side of this point, the male phenotype whose frequency is below the equilibrium point is always at a selective advantage; hence the stability of the equilibrium. This feature of the models can be illustrated by choosing symmetrical parameter values such that $\alpha = \beta$ and $k = h$ or $m = n$. These values always give rise to a stable equilibrium at $w^* = 0.5$. Figures 1 and 2 show the fitness functions with $\alpha = \beta = 0.2$ and with the following sets of values for k and h and m and n.

OD model	CCLK model
$m = n = 2$	$k = h = 2.0$
$m = n = 5$	$k = h = 5.0$
$m = n = 10$	$k = h = 10.0$

The fitness function for the 'A' phenotype only is shown; that for the 'B' phenotype is symmetrical in the reverse direction of frequency. The figures show that the OD and CCLK encounter models produce very similar levels of frequency dependence in the males' sexual advantage. Both, as we have seen, fit the same data almost equally well. The different parametrization of these models has surprisingly little effect. The frequency dependence, as shown by the rate of increase of fitness for a given reduction in frequency, is greater at higher values of the m, n or k, h parameters. This is to be expected because the models converge on the complete preference model as these parameters increase and females become more 'choosy'. This is the point that we wish to emphasize most strongly in this paper. As females become less choosy (with lower values of m, n or k, h), they express their preference with more dependence on male frequency, whereas the resulting selection of the males becomes less frequency dependent. More choosy females (with higher values of m, n or k, h) are more constant in expressing their preference, producing greater frequency dependence in the consequent selection.

The fitnesses become equal at the equilibrium point $w^* = 0.5$ when $f_A = f_B = 1.0$ as expected. At this point there is no variance in male fitness. This fact is relevant to a consideration of the significance of the genetic load under frequency-dependent selection. In models of frequency-dependent natural selection there may also be no variance in fitness at equilibrium. For example, selection of Batesian (palatable) mimics of unpalatable models acts equally on all mimics at equilibrium (Clarke & O'Donald 1962; O'Donald & Barrett 1973).

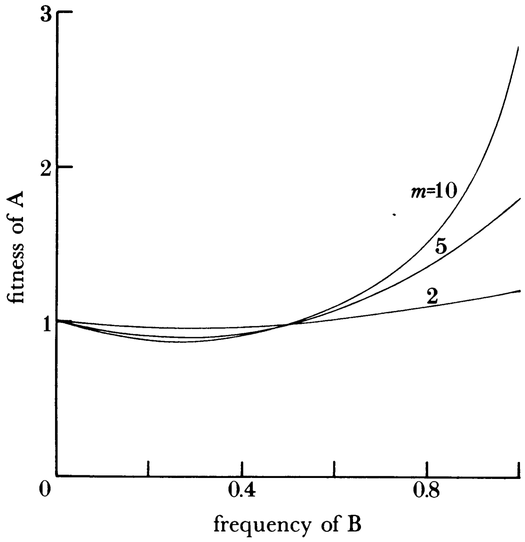

FIGURE 1. Relative fitnesses of phenotype 'A' according to the OD encounter model. The population consists of phenotypes 'A' and 'B'; 20 % of females prefer each phenotype. Fitness functions are shown for three examples of the number of encounters with non-preferred males that a female must make before she is sufficiently stimulated to mate with any male ($m = 2, 5, 10$).

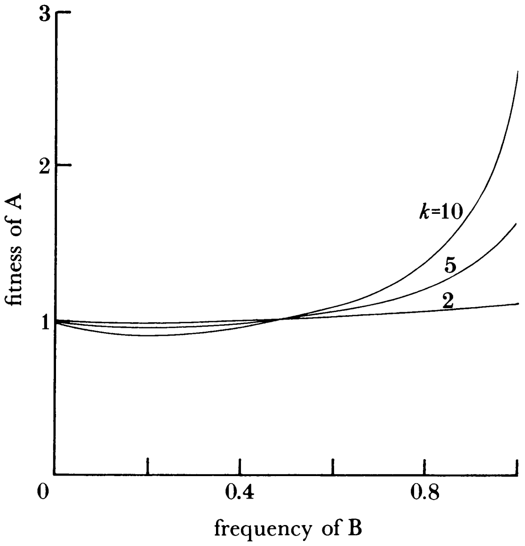

FIGURE 2. Relative fitnesses of phenotype 'A' according to the CCLK model. As in figure 1, the phenotypes 'A' and 'B' are each preferred by 20 % of females. k is the relative probability that a female preferring 'A' will mate with 'A' if she encounters 'A' compared with the relative probability 1.0 that she mates with 'B' if she encounters 'B' ($k = 2, 5, 10$).

At equilibrium, therefore, the variance in fitness and genetic load is zero. But this should not be taken to imply that frequency-dependent selection entails no selective death at equilibrium and hence could maintain any number of polymorphisms. In Batesian mimicry, the mimics still suffer mortality at the equilibrium point; it is just that, at equilibrium, the mortalities of the mimics are proportional to their equilibrium frequencies. Any deviation from equilibrium immediately increases the mortality of the phenotype at increased frequency, thus imposing selection that restores the population to equilibrium. The selective mortality that maintains the polymorphism does not disappear when equilibrium is reached. The genetic load formula merely does not measure it. To measure the selective mortality of Batesian mimics, it would be necessary to formulate a detailed ecological model of the selection to be applied to the corresponding data. The standard genetic load formula for selective mortality can only be applied to selection with constant fitness values.

According to the sexual selection models we have discussed in this paper, the genetic load may really be zero. The males alone are subject to the selection and hence vary in fitness. As in the models of selection for Batesian mimics, the males' fitnesses become equal at equilibrium. But the sexual selection, which maintains the polymorphism, gives rise to no variation in female fitness: no necessary change in female fertility takes place as a result of the process of mate choice. In theory, preferential mating can occur without loss of fitness. If so, sexual selection, which would also include male competition, could indeed maintain any number of polymorphisms. In practice, of course, expressing a preference may well entail some cost to the preferring females: certainly if the preferred males are at low frequency, the search for them will entail a delay in mating that may reduce fertility. Such costs will be greater, when the expression of preference is more nearly complete.

REFERENCES

Charlesworth, D. & Charlesworth, B. 1975 Sexual selection and polymorphism. *Am. Nat.* **109**, 465–470.

Charlesworth, D. & Charlesworth, B. 1980 Frequency-dependence in a model of sexual selection. *Theor. Popul. Biol.* **19**, 163–168.

Clarke, B. & O'Donald, P. 1962 Frequency-dependent selection. *Heredity, Lond.* **19**, 201–206.

Darwin, C. R. 1871 *The descent of man, and selection in relation to sex.* London: John Murray.

Ehrman, L. 1970 The mating advantage of rare males in *Drosophila. Proc. natn. Acad. Sci. U.S.A.* **65**, 345–348.

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

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

Karlin, S. & O'Donald, P. 1978 Some population genetic models combining sexual selection and assortative mating. *Heredity, Lond.* **41**, 165–174.

Karlin, S. & O'Donald, P. 1981 Sexual selection at a multiallelic locus with complete or partial dominance. *Heredity, Lond.* **47**, 209–220.

Kirkpatrick, M. 1982 Sexual selection and the evolution of female choice. *Evolution* **36**, 1–12.

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

Lande, R. 1981 Models of speciation by sexual selection on a polygenic trait. *Proc. natn. Acad. Sci. U.S.A.* **78**, 3721–3725.

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.

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

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

O'Donald, P. 1962 The theory of sexual selection. *Heredity, Lond.* **17**, 541–552.

O'Donald, P. 1967 A general model of sexual and natural selection. *Heredity, Lond.* **22**, 499–519.

O'Donald, P. 1973 Models of sexual and natural selection in polygynous species. *Heredity, Lond.* **31**, 145–156.

O'Donald, P. 1976 Mating preferences and their genetic effects in models of sexual selection for colour phases of the Arctic skua. In *Population genetics and ecology* (ed. S. Karlin & E. Nevo), pp. 411–430. New York: Academic Press.

O'Donald, P. 1978*a* Theoretical aspects of sexual selection: a generalised model of mating behaviour. *Theor. Popul. Biol.* **13**, 226–243.

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

O'Donald, P. 1979 Theoretical aspects of sexual selection: variation in threshold of female mating response. *Theor. Popul. Biol.* **15**, 191–204.

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

O'Donald, P. 1980*b* Sexual selection by female choice in a monogamous bird: Darwin's theory corroborated. *Heredity, Lond.* **45**, 201–217.

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

O'Donald, P. 1983*b* *The Arctic skua. A study of the ecology and evolution of a seabird.* Cambridge University Press.

O'Donald, P. & Barrett, J. A. 1973 Evolution of dominance in polymorphic Batesian mimicry. *Theor. Popul. Biol.* **4**, 173–192.

O'Donald, P., Derrick, M., Majerus, M. E. N. & Weir, J. 1984 Population genetic theory of the assortative mating, sexual selection and natural selection of the two-spot Ladybird, *Adalia bipunctata*. *Heredity, Lond.* **52**, 43–61.

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.

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

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

Petit, C. 1954 L'isolement sexuel chez *Drosophila melanogaster*. Etude du mutant *white* et de son allelomorph *sauvage*. *Bull. biol. Fr. Belg.* **88**, 435–443.

Spiess, E. B. 1983 Do female flies choose their mates? *Am. Nat.* **119**, 675–693.

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

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