FREQUENCY-DEPENDENT SEXUAL SELECTION AS A RESULT OF VARIATIONS IN FITNESS AT BREEDING TIME

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SUMMARY

Darwin's model of sexual selection by variations in fitness at breeding time is generalised to allow for the sexual advantage of the favoured males to be only partial and not complete. If the earlier breeding pairs are the fitter, as Darwin assumed, then the favoured males will always gain a selective advantage; computer simulations show that this selection is frequency-dependent. If a female mating preference determines the sexual advantage of the males, then the proportion α of the females who exercise the mating preference will determine whether the frequency dependence is positive or negative. When α is less than 0.3, the overall selective advantage of the favoured males declines as they increase in frequency: the selection is thus negatively frequency-dependent. Polymorphic equilibria may also become established if natural selection is acting against the sexually favoured character of the males. When α is greater than 0.7, the selective advantage increases rapidly as the favoured males increase in frequency. When earlier pairs are not fitter and fitness at breeding time is distributed symmetrically round the optimum, males favoured as a result of a female mating preference can still gain an advantage even though a proportion of these males will be chosen by the earlier females and form pairs with low fitnesses. This model of sexual selection does not therefore depend on Darwin's assumption that the earlier pairs are the fitter.

1. INTRODUCTION

ACCORDING to Darwin's original theory of sexual selection (Darwin, 1859), some males will gain a selective advantage if they have characteristics that improve their chances of mating. The theory requires polygamy: the stronger males who drive away the weaker collect more females to mate with. The females may also have a mating preference for particular male characteristics. They may prefer to mate with males who have more elaborate sexual displays. Male sexual displays will therefore evolve as a result of the female preference. General models of sexual selection (O'Donald, 1962, 1967) show that it should produce a rapid evolution of both male characters and female preferences. Female preferences in favour of wild-type males are now well known in species of *Drosophila* (see for example Smith, 1956; Faugères, Petit and Thibout, 1971); and Ehrman (1967, 1968) has observed frequency-dependent sexual selection of male *Drosophila* with different chromosomal inversions.

Darwin (1871) also described a model of sexual selection in monogamous animals. Sexual selection could easily take place in a monogamous species provided the males were the more numerous sex. Then the female mating preferences would give an advantage to the preferred males by leaving other males unmated. But this cannot be a general explanation of the evolution of male sexual displays in monogamous species. Darwin's own theory depends on the assumption that pairs who have mated earlier in the breeding season

are fitter than later pairs. For example, if the males of a species of bird establish territories before the females come to breed, then the first females to arrive will mate either with the males who have been most successful in maintaining their territories or with those who are the objects of the female preference. Darwin argued that the earlier females would be the fitter and would rear more offspring. He thought that females who were better nourished would for that reason both breed earlier and be able to rear more offspring. As Fisher (1930) pointed out, the correlation between fitness and early breeding has to be entirely environmental, depending perhaps on the conditions encountered by the females in the previous winter, for if it were partly genetic, the breeding season would also be selected for earliness and earliness would eventually become a disadvantage as the breeding season got earlier.

O'Donald (1972*a*) discussed Darwin's theory in detail and gave data on the breeding success of the Arctic Skua, a colonial sea bird of the North Atlantic, showing that the earlier pairs did have the higher fitnesses. A quadratic relationship between fitness and breeding time fitted the data very well. Since the first pairs to breed had higher fitnesses than the mean fitness, males who may have mated early as a result of favoured sexual characteristics would therefore have gained a selective advantage. The last pairs to breed were much less fit than the mean. If, therefore, only a few of the males had unfavourable sexual characteristics and were left to mate with the last females to breed, they would be at a great selective disadvantage. A sexually favoured character, therefore, would have an increased advantage as it evolved and spread through the population. Thus the selection, as calculated from the quadratic fitness function of breeding time, was found to be strongly and positively frequency-dependent: the selective advantage increased as the sexually favoured males increased in frequency. In this model, as Darwin had assumed, the sexually favoured males all mated before any of the others: their sexual advantage was therefore complete.

The model can be made more general in three ways. In the first, the sexual advantage of the favoured males may be incomplete: only some of them may be successful in the fight to maintain their territories; only some of the females may have a mating preference for a particular male characteristic. In the second generalisation of the model, the relationship between fitness and breeding success may not give an unqualified advantage to the earlier pairs: the breeding season, as suggested by O'Donald (1972*a*), may eventually evolve towards an optimum breeding time which is equal to the mean. The first pairs to breed would then have a lower fitness than the pairs breeding at the mean. A few sexually favoured males would not then get an overall advantage if, for example, the female preference for them were complete and they all mated with the earliest females. To get an advantage when the mean breeding time is the optimum, the female preference must be incomplete so that most of the favoured males are left to mate with females ready to mate at the mean breeding time. Finally, the model may be made more general by allowing for natural as well as sexual selection of the male characteristics. Some preliminary results have been obtained from a computer model that allowed for a partial female preference and a more general distribution of breeding time (O'Donald, 1972*b*). More results, to be described here, have now been obtained from this model and also from models that allow for natural selection as well.

Three particular distributions were used for the breeding times. The first was the empirical distribution observed in the Arctic Skua. The fitness function of the relation between fitness and breeding time was calculated from data on the breeding success of pairs breeding at different times. It is of the form

$$w = 1 - (\theta - x)^2 / \phi,$$

where x is the breeding time. θ is the optimum when the fitness is at a maximum of $w = 1$. The constants θ and ϕ can be calculated from the data (see O'Donald, 1972a). The second distribution of breeding times was assumed to be normal, but with the same mean and variance as the empirical distribution. The optimum breeding time θ and the constant ϕ were assumed to be the same as before. The third distribution was normal like the second, but this time the optimum was assumed to be the mean, at $\theta = \bar{x}$, so that the fitnesses declined symmetrically on either side of the mean: thus the first pairs to breed were as disadvantageous as the last. For all three distributions partial female preferences determined the selective advantage of the favoured males who might at the same time be at a disadvantage as a result of natural selection.

2. EMPIRICAL DISTRIBUTION OF BREEDING TIMES

Table 1 shows the distribution of breeding times in the Arctic Skua according to the number of pairs hatching their first egg in different weeks

TABLE 1
Fitnesses of pairs of Arctic Skuas breeding at different times

Date of 1st hatching	Week	No. pairs	No. chicks fledged	Observed fitness	Theoretical fitness
10-16 June	0	20	32	0.95	0.99075
17-23 June	1	114	192	1.0	0.98857
24-30 June	2	61	92	0.89549	0.90393
1-7 July	3	23	28	0.72283	0.73683
8-14 July	4	3	3	0.59375	0.48726

during the breeding season. The observed fitness shown in the table were calculated from the number of chicks fledged by the different pairs. The values of $\theta = 0.47354$ weeks, and $\phi = 24.254$ were then calculated from the mean and variance in fitness (O'Donald, 1972a). The fitness function $w = 1 - (\theta - x)^2 / \phi$ then gives the theoretical fitnesses. In calculating the selective coefficients of males mating with females breeding at different times, these theoretical fitnesses were used. They give values very close to the values obtained from the empirical fitnesses and have the advantage that the same fitness function can also be used with other distributions of breeding time.

The simplest genetical model is for the sexually favoured character to be determined by a sex-limited dominant gene expressed only in males. If the favoured males have a fitness of 1 and the others a fitness of $1 - s$, then after selection the gene frequency becomes

$$p' = \frac{p - \frac{1}{2}spq^2}{1 - sq^2},$$

where p is the frequency of the gene for the favoured character. Thus the change in gene frequency in a generation is

$$\Delta p = \frac{\frac{1}{2}spq^2}{1 - sq^2}.$$

When s is determined by the sexual advantage of the males, it can be calculated from the relative fitness, w_a , of matings involving the sexually favoured males and the relative fitness, w_b , of other matings. Thus

$$s = 1 - w_b/w_a.$$

If natural selection also affects the two types of male, then independent fitnesses, $1 - S$ and 1 , are defined in the model which act on the males after the sexual selection has taken place.

A proportion α of the females are assumed actually to exercise a mating preference for the sexually favoured males. In the models studied so far, this proportion is constant. More general models can be set up in which the proportion α is genotypically determined by alleles at another locus. Thus if the allele B determines the mating preference, females who are BB or Bb prefer to mate with the sexually favoured males. Then the proportion α will itself change as the advantageous males increase in frequency. The allele B will be selected because it will be passed to the sons of the preferred fathers and these sons will also tend to possess the sexually favoured character like their fathers before them. A model of sexual selection in a polygamous species (O'Donald, 1967) showed that an association is built up between the alleles for the female preference and those for the male character. In certain circumstances both could evolve very rapidly. The present model, which doesn't allow for the evolution of the female preference, is thus likely to underestimate the possible rates of sexual selection. However, the selection of a female preference is unlikely to be as rapid as in a polygamous species when a large number of females with the mating preference gene can all mate with a single male who has the preferred character.

Given a value for α , the selective values of both favoured males and others can be calculated. Since α is the proportion of females exercising the mating preference, they will all mate with the preferred males if they can. At any interval in the breeding season, a proportion of females given by the distribution of breeding times will be ready to mate. If this proportion is p_i , then αp_i is the fraction of the females who will exercise their mating preference in the i th interval in the breeding season. Therefore a fraction $(1 - \alpha)p_i$ of the females do not exercise the mating preference and these females are assumed to mate at random with both the favoured males and the rest. Given the fitnesses of matings in each interval, the mean fitness of matings involving the two types of males can be calculated. The details of the computer program are given in the appendix.

Table 2 gives the results of the computer simulations of selection for a dominant gene starting at a frequency 0.001. The female preference for the males who possess the gene varies from $\alpha = 0.1$ to $\alpha = 1.0$. The results of the computation when $\alpha = 1.0$ are identical to those given by O'Donald (1972a). Fig. 1 shows these changes in the selective coefficients for values of α of 0.2, 0.4, 0.6 and 0.8. When $\alpha = 1.0$ and the sexual advantage of the males is complete, the selective coefficient increases rapidly as the favoured males themselves increase in frequency. The selection is positively frequency-

TABLE 2
Gene frequencies and sexual selective coefficients of a dominant male character with no natural selection

No. generations	Proportion of females, α , exercising the mating preference									
	$\alpha = 0.1$		$\alpha = 0.2$		$\alpha = 0.4$		$\alpha = 0.6$		$\alpha = 0.8$	
	p	s	p	s	p	s	p	s	p	s
1	0.00103	0.0590	0.00103	0.0590	0.00103	0.0590	0.00103	0.0590	0.00103	0.0590
50	0.00467	0.0594	0.00467	0.0594	0.00467	0.0594	0.00467	0.0594	0.00467	0.0594
100	0.0212	0.0599	0.0216	0.0603	0.0218	0.0612	0.0218	0.0615	0.0218	0.0615
120	0.0384	0.0577	0.0394	0.0621	0.0400	0.0626	0.0403	0.0631	0.0403	0.0638
140	0.0623	0.0472	0.0716	0.0646	0.0731	0.0666	0.0738	0.0669	0.0742	0.0676
160	0.0901	0.0368	0.118	0.0539	0.133	0.0755	0.135	0.0759	0.136	0.0762
180	0.118	0.0295	0.171	0.0442	0.222	0.0691	0.243	0.0894	0.247	0.0989
200	0.145	0.0245	0.223	0.0367	0.322	0.0631	0.380	0.0949	0.418	0.119
220	0.170	0.0198	0.271	0.0311	0.411	0.0563	0.512	0.0907	0.594	0.148
240	0.195	0.0188	0.314	0.0276	0.484	0.0505	0.611	0.0895	0.714	0.159
260	0.218	0.0170	0.353	0.0251	0.544	0.0469	0.682	0.0848	0.794	0.167
300	0.262	0.0145	0.422	0.0220	0.633	0.0430	0.771	0.0807	0.868	0.163
350	0.311	0.0126	0.492	0.0198	0.709	0.0407	0.833	0.0788	0.911	0.162
400	0.355	0.0113	0.549	0.0184	0.761	0.0396	0.869	0.0779	0.933	0.161
600	0.494	0.0089	0.696	0.0162	0.864	0.0381	0.932	0.0770	0.967	0.161
1000	0.657	0.0075	0.824	0.0152	0.930	0.0376	0.966	0.0768	0.984	0.161

p is the gene frequency of the allele that determines the sexually favoured character of the males and it was given the initial value of 0.001 in these computations.

FIG. 1.—Selective coefficients of the sexually favoured male phenotype as a result of female mating preference when different proportions, α , of the females exercise the preference. The proportions of the favoured male phenotype are shown alongside the graphs of the selective coefficient at particular generation times.

dependent for all values of α greater than about 0.7 and the frequency dependence increases as α increases. But just the opposite happens when α is less than about 0.3. Then the selection is negatively frequency-dependent and for very small values of α the selective coefficient becomes very small as the sexually favoured males become common. In the end they are at only a very slight selective advantage. Around the values of $\alpha = 0.5$ there is little frequency-dependent effect in the selection. The decline in selective advantage when α is small suggests that a polymorphism could be maintained if natural selection opposes the sexual selection. It is likely that it will do so because characters for sexual display act as sexual advertisements for the females and must also attract the attention of predators. The more extreme sexual adornments of the pheasant or peacock, for example, must also be a considerable hindrance when escaping from predators. If the natural selective coefficient is a constant, it must at the start of selection be less than the sexual selective coefficient, for if it were greater the gene for the sexually favoured character would quickly be eliminated. If α is small and the sexual selection is negatively frequency-dependent, a polymorphism can be set up if the sexual selective coefficient declines to the point where it exactly equals the natural selective coefficient. Such an equilibrium must be stable. If there were a further increase in the frequency of the favoured males, the sexual selective coefficient would decline still further and become less than the natural selective coefficient. Natural selection would therefore reduce the frequency of the males until the equilibrium was restored. If the frequency of the males became less than the equilibrium frequency, the sexual selective coefficient would increase and bring them back to equilibrium again.

Tables 3 and 4 show the equilibrium frequencies and sexual selective coefficients for different values of α and the natural selective coefficient S .

TABLE 3
Equilibrium gene frequencies when natural selection opposes sexual selection

Values of α	Values of natural selective coefficient					
	0.01	0.02	0.03	0.04	0.05	0.06
0.05	0.1733	0.0825	0.0537	0.0384	0.0244	0
0.10	0.4202	0.1826	0.1176	0.0827	0.0544	0
0.15	1.0	0.3096	0.1931	0.1353	0.0961	0
0.20	1.0	0.4854	0.2860	0.2000	0.1485	0
0.25	1.0	0.7983*	0.4062	0.2827	0.2038	0
0.30	1.0	1.0	0.5797	0.3815	0.2745	0
0.35	1.0	1.0	1.0	0.5165	0.3779	0
0.40	1.0	1.0	1.0	0.7444	0.4979	0
0.45	1.0	1.0	1.0	1.0	0.6873	0
0.50	1.0	1.0	1.0	1.0	1.0	0

The frequencies enclosed by the solid line are those at which a stable equilibrium has been established. The frequency marked * had not quite reached equilibrium at 10,000 generations and the true equilibrium frequency will be greater.

TABLE 4
Sexual selective coefficients at the equilibrium with natural selection

Values of α	Values of natural selective coefficient					
	0.01	0.02	0.03	0.04	0.05	0.06
0.05	0.01	0.02	0.03	0.04	0.05	0.0589
0.10	0.01	0.02	0.03	0.04	0.05	0.0589
0.15	0.0105	0.02	0.03	0.04	0.05	0.0589
0.20	0.0147	0.02	0.03	0.04	0.05	0.0589
0.25	0.0194	0.02	0.03	0.04	0.05	0.0589
0.30	0.0247	0.0247	0.03	0.04	0.05	0.0589
0.35	0.0306	0.0306	0.0306	0.04	0.05	0.0589
0.40	0.0374	0.0374	0.0374	0.04	0.05	0.0589
0.45	0.0451	0.0451	0.0451	0.0451	0.05	0.0589
0.50	0.0540	0.0540	0.0540	0.0540	0.0540	0.0589

When equilibrium is reached the natural and sexual selective coefficients are equal. Elsewhere the sexual selective coefficient is shown when the favoured males are at the point of fixation or elimination.

A range of different initial gene frequencies was used in order to demonstrate the stability of the equilibrium. Table 4 shows that in a polymorphism the sexual selective coefficients reach exact agreement with the natural selective coefficients. Agreement in the eight significant figure is reached at between 2000 and 10,000 generations. The longer times are required when the selective coefficients are small or changing slowly. In one case the final equilibrium had not been reached after 10,000 generations.

So long as the natural selective coefficient, S , is less than 0.059, the sexually favoured males have the overall advantage at the start. They increase in frequency, either to a polymorphic equilibrium if the sexual selective coefficient, s , decreases sufficiently to equal S , or to complete fixation if s never gets sufficiently small. If S is greater than 0.059, the sexually favoured males are at an initial disadvantage since S is greater than s and they are therefore eliminated. When $S = 0.06$, the sexual selective coefficient shown in table 4 is always $s = 0.0589$. This is the value of the sexual selective coefficient when the favoured males are at the point of being eliminated. If α is greater than 0.5, then the sexual selection becomes positively frequency-dependent. Therefore, provided s is greater than S at the start of selection, the sexually favoured males will necessarily be selected to complete fixation, and they will always be eliminated when S is greater than s .

3. NORMAL DISTRIBUTION OF BREEDING TIMES

So far the empirical distribution of breeding times in the five weeks of the breeding season of the Arctic Skua has been used to calculate the sexual selective coefficient, s , given the theoretical fitness of the pairs in each week. If many more data on breeding times were available, the distribution could be constructed in intervals of one day instead of one week. A smoother distribution would then be obtained. Such a distribution can be constructed theoretically if it is assumed that breeding times are normally distributed. The mean and variance found for the empirical distribution of breeding times can be used to calculate the distribution from the distribution of a standard normal deviate. Since these values are in terms of weeks, the normal distribution can most easily be constructed in intervals of one-seventh of a week. The empirical distribution cuts off sharply at week 0, but the normal distribution extends into week -1 because of its necessarily longer tail. The fitnesses of each interval of one-seventh of a week can still be calculated from $w = 1 - (\theta - x)^2/\phi$, where θ and x are in weeks. Using the values of $\theta = 0.47354$ and $\phi = 24.254$, we get the fitness and cumulative normal probabilities which are given for every third day in table 5. In the actual calculation of the sexual selective coefficients the values of fitness and probability at each day were used.

These values give a mean fitness of 0.92699. This is greater than the fitnesses of the first few pairs to breed. Not until day 4 does the fitness of the pairs equal the mean fitness. The mean fitness in the first six days of breeding is less than the mean fitness of the rest of the population. But the mean fitness of pairs breeding in the first 7 days is greater than the mean of the rest of the population. If all the sexually favoured males were to be mated before any of the others, there must be enough of them to provide mates for females who mate up to the seventh day. Only then will they gain a selective

advantage by having a mean fitness greater than the rest of the males. The fitness of the first 0.662 per cent. of pairs to breed is 0.927 and hence greater than both the mean fitness of the whole population and the remaining 99.338 per cent. of pairs. Therefore, if the sexually favoured males are at a frequency of 0.00662, they will be at an advantage even when the female mating preference is complete. If the males are at a lower frequency they can still gain an advantage as a result of a partial female preference. If only a fraction of the favoured males mate with the earliest females, enough of them will usually be left to mate with later females and form pairs of higher fitness breeding nearer the optimum.

Table 6 shows the course of sexual selection over a large number of generations when the initial gene frequency is 0.001. The favoured males

TABLE 5
Hypothetical normal distribution of breeding times

Time in days given as 7ths of a week	Cumulative probability	Theoretical fitness	No. days from origin
-10/7	0.00017	0.85083	0
-1	0.00189	0.91047	3
-4/7	0.00898	0.95498	6
-1/7	0.03177	0.98433	9
2/7	0.08876	0.99854	12
5/7	0.19975	0.99761	15
8/7	0.36808	0.98153	18
11/7	0.56690	0.95030	21
2	0.74986	0.90393	24
17/7	0.88095	0.84241	27
20/7	0.95412	0.76575	30
23/7	0.98592	0.67394	33
26/7	0.99669	0.56698	36
29/7	0.99952	0.44488	39
31/7	1.00000	0.35506	41

The days are given as 7ths of the weeks by which the empirical distribution of breeding times was tabulated, but the normal distribution extends into week -1. The theoretical fitnesses are given by $w = 1 - (\theta - x)^2/\phi$ where $\theta = 0.47354$ and $\phi = 24.254$ which is the same fitness function as was used with the empirical distribution of breeding times.

start at a phenotypic frequency of 0.001999, which is considerably less than the frequency needed for a selective advantage to be gained with complete female preference. Thus at the higher values of α the sexually favoured males are selectively disadvantageous. Selection would have to start with the males at higher frequencies if they were to gain an initial selective advantage at the higher values of α : as α increases, the initial selective coefficient decreases, eventually becoming negative at between $\alpha = 0.3$ and $\alpha = 0.35$. Once the males have started to spread through the population, the selective coefficient necessarily increases since the earliest females, whose fitness is less than the mean, have less effect on the average fitness of the favoured males. But then, as the favoured males become common, their selective coefficient declines again, since the selection becomes negatively frequency-dependent in the same way as it does for the empirical distribution of breeding times at low values of α .

These results show that changes in the distribution of breeding times and in the proportion of females exercising the mating preference can make

TABLE 6
Gene frequencies and sexual selective coefficients when breeding times are normally distributed
 Proportion of females, α , exercising the mating preference

No. generations	$\alpha = 0.05$		$\alpha = 0.10$		$\alpha = 0.15$		$\alpha = 0.20$		$\alpha = 0.25$		$\alpha = 0.30$		$\alpha = 0.35$	
	p	s	p	s	p	s	p	s	p	s	p	s	p	s
1	0.0010	0.0445	0.0010	0.0290	0.0010	0.0187	0.0010	0.0112	0.0010	0.0051	0.0010	0.0001	0.0010	-0.0049
50	0.0041	0.0646	0.0027	0.0501	0.0019	0.0349	0.0015	0.0214	0.0012	0.0046	0.0010	0.0003	0.0008	-0.0091
100	0.0214	0.0575	0.0126	0.0675	0.0062	0.0577	0.0032	0.0396	0.0017	0.0190	0.0010	0.0006	0.0006	-0.0189
200	0.108	0.0206	0.144	0.0320	0.127	0.0486	0.0633	0.0680	0.0110	0.0592	0.0011	0.0026	0.0001	-0.0692
300	0.192	0.0123	0.297	0.0178	0.351	0.0245	0.350	0.0342	0.216	0.0556	0.0014	0.0092	0	-0.0895
500	0.327	0.0078	0.498	0.0121	0.599	0.0170	0.658	0.0229	0.671	0.0300	0.0658	0.0733	0	-0.0895
700	0.429	0.0064	0.619	0.0106	0.720	0.0155	0.778	0.0213	0.808	0.0278	0.667	0.0384	0	-0.0895
1,000	0.541	0.0054	0.726	0.0098	0.812	0.0149	0.859	0.0206	0.885	0.0272	0.863	0.0349	0	-0.0895
2,000	0.736	0.0046	0.866	0.0092	0.915	0.0144	0.939	0.0203	0.953	0.0269	0.957	0.0344	0	-0.0895
3,000	0.820	0.0044	0.914	0.0091	0.946	0.0144	0.962	0.0203	0.971	0.0269	0.975	0.0343	0	-0.0895
5,000	0.893	0.0044	0.950	0.0091	0.969	0.0144	0.978	0.0202	0.983	0.0268	0.986	0.0343	0	-0.0895
7,000	0.925	0.0043	*	*	0.978	0.0144	0.985	0.0202	0.988	0.0268	0.991	0.0343	0	-0.0895
10,000	0.948	0.0043	*	*	0.985	0.0143	0.989	0.0202	0.992	0.0268	0.994	0.0343	0	-0.0895

The spaces in the table marked * are where data are missing for these generations.

all the difference to the outcome of the sexual selection. If there is a small proportion of very early breeders with fitnesses less than the mean, then sexual selection can start only if the female preference is not so great that all the favoured males mate with the earliest females. If there is only a slight female preference, a higher proportion of the favoured males mate later to form pairs with the higher mean fitness and thus obtain a selective advantage.

TABLE 7
Equilibrium gene frequencies when natural selection opposes sexual selection and breeding times are normally distributed

Values of α	Values of natural selective coefficient		
	0.01	0.02	0.03
0.05	0.2456	0.1139	0.07182
0.10	0.6834	0.2606	0
0.15	1.0	0	0
0.20	1.0	0	0
0.25	0	0	0

In these calculations the fitness function was the same as in the calculations using the empirical distribution of breeding times with $\theta = 0.47354$ and $\phi = 24.254$.

TABLE 8
Sexual selective coefficients at equilibrium with natural selection when breeding times are normally distributed

Values of α	Values of natural selective coefficient		
	0.01	0.02	0.03
0.05	0.01	0.02	0.03
0.10	0.01	0.02	-0.08952
0.15	0.01435	-0.08952	-0.08952
0.20	0.02024	-0.08952	-0.08952
0.25	-0.08952	-0.08952	-0.08952

The negative selective coefficients are those when the sexually favoured males are on the point of being eliminated from the population. They are negative because, when breeding times are normally distributed, the earliest pairs have a lower fitness than the mean and are thus at an overall disadvantage.

The later females, breeding nearer to the mean breeding time, are more common than the earliest females. Thus, if the mating preference is small, most of the favoured males are left to mate with the most fit females. This explains why, as α decreases, the initial selective coefficient increases. There are here two frequency-dependent effects. The initial selective coefficient is dependent upon α —the frequency of the expression of the mating preference. Once the males have increased in frequency to a point at which they must gain a selective advantage whatever the value of α , then

the selection is negatively frequency-dependent if α is small and positively frequency-dependent if α is large.

Genetic polymorphisms can also be established at equilibrium with natural selection when breeding times are normally distributed. This can happen only if the sexual selective coefficient starts at a higher value than the natural selective coefficient and then decreases as the favoured males spread through the population until they reach a balance with the natural selection that is acting against them. The conditions for a stable polymorphism are now rather more restrictive than when breeding times had the empirical distribution of the Arctic Skua. Since, in our example of a normal distribution, the initial advantage by sexual selection decreases as α increases, the natural selective coefficient must be small to produce a disadvantage less than the advantage of the sexual selection. If the disadvantage of the natural selection is initially greater than the sexual advantage, the sexually favoured males are, of course, always eliminated. Tables 7 and 8 show the values of gene frequencies and sexual selective coefficients at

TABLE 9
*Initial and final coefficients of sexual selection when
breeding times are normally distributed and favoured
males have an unconditional advantage*

Values of α	Sexual selective coefficient	
	Initial value	Final value
0.2	0.060680	0.020248
0.4	0.049776	0.052489
0.6	0.041517	0.110625
0.8	0.035239	0.237876
1.0	0.030991	0.616973

equilibrium with natural selection. Only the smallest values of α and the natural selective coefficient now give rise to polymorphic equilibria.

In all these calculations with normally distributed breeding times, the sexually favoured males were determined by a dominant gene starting at a frequency of 0.001. They only gain an initial selective advantage if α is less than 0.35: less than 35 per cent. of the females can exercise the mating preference. But if the males have a phenotypic frequency greater than 0.00661 they will gain an unconditional advantage: when the first pairs are at a frequency of 0.00661 they have a fitness just equal to the rest, and at a higher frequency they have a fitness greater than the rest. Table 9 gives the initial and final selective coefficients under sexual selection when the gene frequency for the favoured male character starts at $p = 0.01$. It shows that the sexual selection is very similar to that for the empirical distribution of breeding times. There is a very strong positive frequency dependence at the higher values of α , but the initial selective coefficient is still dependent on α and decreases as α increases. Further computations at other frequencies show these effects are general. The initial selective coefficient depends inversely on α ; but the subsequent selection, provided the favoured males have the initial advantage, is negatively frequency-dependent for small values of α and positively frequency-dependent for large values.

4. NORMALLY DISTRIBUTED BREEDING TIMES WITH THE OPTIMUM AT THE MEAN

In Darwin's and Fisher's original discussions of the theory of sexual selection, they assumed that the earliest pairs must be fitter than the mean. As we have shown in the previous section, this is a necessary assumption if the sexual selection is complete. When the earliest pairs have a fitness less than the mean, then the favoured males can gain an advantage only if they are sufficiently numerous to form pairs with a higher fitness than the rest or if the sexual selection by the females is incomplete and a sufficient fraction of the favoured males is left by the earliest females to mate later and form pairs fitter than the mean. These facts suggest that in certain circumstances the males could gain an advantage even when the fitness function is symmetrical round the mean breeding time. The fitness function will now be $w = 1 - (\bar{x} - x)^2 \phi$. If the breeding times are normally distributed, the first pairs to breed will be at as great a disadvantage as the last.

Suppose there is a complete female preference ($\alpha = 1.0$) and all the sexually favoured males mate first. If they are at a frequency of less than 0.5, they will form pairs whose average fitness is less than that of the rest for they are all breeding before the mean and optimum time. Thus they will be at a disadvantage. If they are at a frequency of 0.5 exactly, they will form pairs breeding right up to the mean and have exactly the same fitness as the rest since the distribution of fitness is symmetrical round the mean. They will have no selective advantage or disadvantage. Above a frequency of 0.5 they will have an advantage. If the preference is not complete and only some of the sexually favoured males mate with the earlier females, enough may be left to mate with the females breeding round the mean to give the favoured males an advantage even when they are at frequencies of less than 0.5. In the previous calculations of selective coefficients with normally distributed breeding times, the optimum was well in advance of the mean breeding time and an advantage was gained over a wide range of frequencies and values of α . When the optimum is at the mean, it is to be expected that the range of values for a selective advantage to be obtained will be much more restricted. The values of α will probably have to be smaller or the initial frequencies of the males larger for them to gain an advantage. Table 10 shows the initial and final values of the selective coefficients for different initial gene frequencies and values of α . The table shows that at low initial frequencies the values of α must be almost equally low for the favoured males not to be at a disadvantage. When the initial frequency is $p_0 = 0.001$, the change to selective disadvantage occurs at between $\alpha = 0.0022$ and $\alpha = 0.0023$. When $p_0 = 0.01$, the change is between $\alpha = 0.022$ and 0.023.

At these low values of α , the selection is of course very slow indeed. Table 11 shows the gene frequencies and selective coefficients when $p_0 = 0.01$ and $\alpha = 0.01$. For such low values of α , the selection is of course negatively frequency-dependent. And with such small selective coefficients which then get smaller as the selection proceeds, the selection is necessarily very slow and gets slower. Thus it appears to be gradually coming to a halt long before the gene for the favoured male character has even reached 50 per cent. Presumably the selective coefficient will tend to some very small value but remain positive. A sort of polymorphism is established simply because the selection has almost stopped. Genetic drift will then mainly

TABLE 10

Initial and final selective coefficients when pairs breeding at the mean are the fittest

Values of α		Initial gene frequency for the favoured males				
		0.001	0.01	0.1	0.2	0.3
0.001	s_0	0.005287	—	—	—	—
	s_n	0.000205	—	—	—	—
0.002	s_0	0.001505	—	—	—	—
	s_n	0.000223	—	—	—	—
0.003	s_0	-0.005024	—	—	—	—
	s_n	-0.5013	—	—	—	—
0.01	s_0	—	0.005424	—	—	—
	s_n	—	0.000303	—	—	—
0.02	s_0	—	0.001681	—	—	—
	s_n	—	0.000439	—	—	—
0.03	s_0	—	-0.004897	—	—	—
	s_n	—	-0.5013	—	—	—
0.1	s_0	—	—	0.006998	0.005212	0.003751
	s_n	—	—	0.001942	0.001947	0.001939
0.2	s_0	—	—	0.003822	0.009333	0.008693
	s_n	—	—	0.004825	0.004824	0.004824
0.3	s_0	—	—	-0.003263	0.009548	0.01245
	s_n	—	—	-0.5013	0.009141	0.009141
0.4	s_0	—	—	—	0.007303	0.01412
	s_n	—	—	—	0.01559	0.01559
0.5	s_0	—	—	—	0.003760	0.01390
	s_n	—	—	—	0.02537	0.02537
0.6	s_0	—	—	—	-0.003706	0.01254
	s_n	—	—	—	-0.5013	0.04055
0.7	s_0	—	—	—	—	0.01032
	s_n	—	—	—	—	0.06505
0.8	s_0	—	—	—	—	0.007562
	s_n	—	—	—	—	0.1067
0.9	s_0	—	—	—	—	0.004506
	s_n	—	—	—	—	0.1827
1.0	s_0	—	—	—	—	0.001209
	s_n	—	—	—	—	0.3339

The selective coefficients were not calculated for the higher frequencies and smaller values of α and for the higher values of α when the selective coefficients had become negative. s_n is the selective coefficient after 10,000 generations of selection.

TABLE 11

Rate of sexual selection when pairs breeding at the mean are the fittest

Generation	Gene frequency	Selective coefficient
1	0.01	0.005424
20	0.01052	0.005410
50	0.01139	0.005350
100	0.01295	0.005130
200	0.01639	0.004491
500	0.02753	0.002870
1,000	0.04601	0.001738
2,000	0.08143	0.001001
5,000	0.1764	0.000486
10,000	0.3041	0.000303

determine the gene frequencies. However, if the gene frequency were reduced by drift, the result would be to increase the selective coefficient. This would resist any tendency towards the elimination of the gene by drift. Genetic drift could therefore reinforce the very feeble effects of selection but it could not oppose and overcome them for they would then increase to oppose and overcome the drift.

5. DISCUSSION

When the breeding times are given by the empirical distribution found for the Arctic Skua, sexual selection always gives a selective advantage to the favoured males. It must do so because whatever proportion of these males mate with the fittest and earliest females they must have a higher mean fitness than the rest of the males. Since the selection is negatively frequency-dependent at the lower values of α , opposing natural selection can produce a stable equilibrium if the point is reached when the natural and sexual selection exactly balance each other. A considerable range of selective coefficients leads to polymorphisms. When the breeding times are normally distributed, the earlier pairs of mates may be less fit than the mean, depending on when the optimum breeding time occurs. If it is much earlier than the mean, the earlier pairs will generally be the fitter although the very earliest pairs may be less fit. If this is so, sexual selection will generally take place provided the males are at a sufficient frequency to form pairs with a mean fitness higher than the rest. They will always have the higher fitness if their sexual advantage is only partial and most of them are left by the earliest females to mate later with females breeding at the optimum time.

This generalisation of the model to allow for only partial sexual advantage shows that even when the optimum is at the mean breeding time, sexual selection can still take place. However, either the favoured males have to be at higher frequencies when the selection starts or the female mating preferences have to be only very slightly in their favour. It is of course more realistic to assume that the mating preference itself will be partly under genetic control. If so, it too will evolve as the males who are favoured increase in frequency. As shown by O'Donald (1967), the mating preference genes will be selected by the advantage possessed by the sons of the females who exercised the mating preference. It may therefore be assumed that the mating preference genes will be rare at first but increase as selection proceeds. Sexual selection should therefore be slow at first but always give an advantage to the favoured males whatever the initial distribution of fitness and breeding time. The female mating preference can never increase as rapidly as the males which are favoured, for the selection of the preference must occur entirely through the sons of the females who exercised the preference. And the sons will probably, but not necessarily, possess the favoured genotypes. The female preference cannot therefore evolve as fast as the sexually favoured male character. It follows that the selective advantage of the males should increase as a result of the selection for α and this will not lead to the males' becoming disadvantageous when the fitnesses are symmetrically distributed round the mean breeding time. The males would certainly be disadvantageous if α were too high initially. But provided α is small enough for them to have the initial advantage, their advantage will be retained: α could not evolve fast enough to produce a disadvantage since the favoured males must always be evolving faster.

This argument is relevant only when the optimum breeding time occurs near to the mean. If it occurs well before the mean, there will always be a selective advantage of the favoured males in the evolutionary circumstances at the start of the sexual selection. The argument does show, however, that Darwin's model of sexual selection in monogamous species is much more general than he thought and does not necessarily depend on the distribution of fitness and breeding time which Darwin postulated. Darwin did not consider the possibility of partial female mating preferences. But when these are allowed for in the model, not only can sexual selection take place without an advantage being possessed by the earlier breeders, but also a number of interesting frequency-dependent effects are revealed which may give rise to stable polymorphisms.

Two further possibilities should be mentioned. Ehrman (1967, 1968) showed that the female mating preferences themselves could be frequency-dependent, the females preferring to mate with males who possessed the rarer of certain chromosomal polymorphisms in *Drosophila pseudoobscura*. Thus, in addition to any evolutionary change in the value of α , α might get larger when the favoured males are rare and get smaller as they become common. This would produce larger selective coefficients at the start of selection. But when the optimum breeding time occurs at the mean, the initial selective advantage would be reduced or even turned into a disadvantage. Perhaps it is more likely that the opposite effect would be observed in the birds and mammals to which this theory more realistically applies. Predators often avoid rare or unusual prey (Coppinger, 1970) and if a female approaches the male as a predator to its prey, the rarer males, who will later become highly advantageous, may at first have only a slight mating preference in their favour.

Although throughout this discussion it has been assumed that the sexual selection occurs as a result of female mating preference, direct selection between male and male can also occur and will be selected in the same way. Male display can act as a threat to other males as well as a sexual stimulus to the females. No doubt the threat may not be a complete deterrent, just as the females may not all exercise a mating preference. And the same will be true for any character that leads to a greater chance of mating by particular males. However, if α is determined by a gene that produces a partly successful threat display, α will not itself evolve as the more successful males become common. Modifiers of the expression of the gene would have to be selected if the threat display is to become more effective.

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6. APPENDIX

The sexual selective coefficient is calculated in the computer program in each generation. The sexually favoured males are called phenotype A and the rest are phenotype B. Y is the proportion of A males and $1 - Y$ the proportion of B males. In each breeding period (of a week or a day) there is a fraction Y_A of A males and Y_B of B males left to mate. Thus in the first breeding period $Y_A = Y$ and $Y_B = 1 - Y$. $P(i)$ is the proportion of females who will breed in the i th period. Of these a fraction ALPHA

prefer to mate with the A males and the rest of the females mate at random. $W(I)$ is the fitness of the pairs in the i th breeding period. That part of the Fortran routine which calculates the fitness of the A and B males is then as follows:

```

C    YA is the fraction of A males and YB the fraction of B males
      WA = 0.
      WB = 0.
      DO 33 I = 1, N
      XA = ALPHA*P(I)
C    XA is the fraction of females in the  $i$ th breeding period who prefer
      to mate with the A males
      XB = P(I) - XA
C    XB is the fraction of females in the  $i$ th breeding period who mate
C    at random with both A and B males
      If (YA - XA) 31, 32, 32
C    If YA.LESS.XA then all A males are mated to the females who
C    exercise their preference for the A males. If YA.GR.XA then
C    XA of the A males are mated to the females with the preference
C    and YA - XA of the A males mate at random
C    Thus XA females mate with A males and YA + YB - XA males
C    remain to be mated
31    WA = WA + W(I)*YA
      WB = WB + W(I)*(XA + XB - YA)
      YB = YB - XA - XB + YA
      YA = 0.
      GOTO 33
32    ZA = (YA - XA)/(YA + YB - XA)
      ZB = YB/(YA + YB - XA)
C    ZA is the proportion of A males who mate at random and ZB
C    is the proportion of B males who mate at random
      WA = WA + W(I)*XA + W(I)*XB*ZA
      WB = WB + W(I)*XB*ZB
      YA = YA - XA - XB*ZA
      YB = YB - XB*ZB
33    CONTINUE
      WA = WA/Y
      WB = WB/(1. - Y)
C    WA and WB are now the relative fitnesses of the A and B males.

```

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