

MATING PREFERENCES AND SEXUAL SELECTION IN THE ARCTIC SKUA

P. O'DONALD, N. S. WEDD and J. W. F. DAVIS

Department of Genetics, University of Cambridge, Milton Road, Cambridge CB4 1XH

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SUMMARY

The relationship between breeding time and fitness in the Arctic skua is described in terms of a fitness function estimated from the empirical data. There is no significant variation in the fitness function between pairs who have bred together for different numbers of years. Sexual selection takes place between the different colour phases of males, for among new pairs the pale-phased males breed later on average and with a greater variance in breeding time than the dark and intermediate males. The sexual selective coefficients were calculated from the fitness function using the distributions of breeding times of males in new pairs. Pale males have a relative disadvantage of 0.07 and intermediates a relative disadvantage of 0.03 compared to dark males. The overall selective coefficients calculated from the empirical values of the fitness of all pairs are 0.18 and 0.16 for pale and intermediate males respectively. There is no significant evidence for selection between different phases of females. Models of the mechanism of sexual selection by female mating preferences are fitted to the distributions of breeding time. About 50 per cent of females must exercise mating preferences to maintain the differences observed. The predictions of the models are discussed in relation to the data at present available.

1. INTRODUCTION

THE Arctic skua is a sea bird that breeds in colonies from the North of Scotland up into the Arctic Circle. It is polymorphic with pale, intermediate and dark phases in its populations. The frequencies of the phases form a cline with pale phases generally more abundant in the northern parts of the range and dark phases more abundant in the southern parts. It breeds monogamously, though about 15 per cent of birds mating together for the first time change their mates in the next breeding season. After a pair have bred together for 2 or 3 years, however, they then normally stay together.

The colony of Arctic skuas on Fair Isle in the Shetlands has been intensively studied for many years. The colour phases of the birds, their breeding time and breeding success and their changes of mate were recorded in detail. The data, which have already been partially analysed (O'Donald, 1962, 1972*a, b, c*; Berry and Davis, 1970), suggest that sexual selection may favour the darker males. Because the Arctic skua is monogamous, sexual selection cannot take place simply as a result of the favoured males mating with more females than the others. To gain an advantage in a monogamous species, a sexually favoured male must mate with a female who will bear him more offspring. Darwin (1871) put forward a subtle theory of how this could happen. He suggested that the females who are the first to breed at the start of the breeding season do so because they are in

a better nourished state than the others who breed later. For the same reason they would also be able to rear more and fitter offspring. The variation in the breeding condition of females would depend on how well they had survived the previous winter. The males who gained an advantage would then be those whom the females preferred to mate with. Or by direct competition with other males for territories, they might have the first choice of the females who were ready to breed. Thus they would gain a selective advantage by mating with the earlier females who would then bear them more offspring. O'Donald (1962) showed that, as Darwin's theory requires, clutch size and fledging success are greater among the earlier pairs of Arctic skuas. He later analysed the data (O'Donald, 1972*a*) in terms of a "fitness function" of the relationship between breeding time, measured by the date of hatching of the first chick, and fitness, measured by the number of chicks a pair managed to fledge successfully. A computer model of Darwin's theory, using the fitness function calculated for the breeding times of the Arctic skua, showed that the sexual selection is necessarily frequency-dependent. It is positively frequency-dependent if most of the females have a mating preference for a particular male phenotype: the selective advantage of the favoured males then increases as they increase in frequency. But if only a few of the females have mating preferences, the selection is negatively frequency-dependent, the selective advantage declining as the favoured males increase and spread through the population.

Berry and Davis (1970) in their analysis of the data showed that among pairs breeding together for the first time darker males tend to breed earlier: dark males breed on average before the intermediates who breed before the pales. There is no significant difference, however, between the mean breeding times of the different phases of female. O'Donald (1972*c*) used Berry and Davis's values of the means and variances of the different phases of males to calculate the selective coefficients of the sexual selection, assuming the fitness function was the same for all pairs. If the dark-phased males are given a relative fitness of one and a selective coefficient of zero, the selective coefficients of intermediates and pales, measured relative to the darks, are 0.13 and 0.34 respectively. Since new pairs are about 36 per cent of all pairs the overall selective coefficients of intermediates and pales are 0.047 and 0.12 by this calculation.

In this paper, the whole of the data, collected on Fair Isle, is fully analysed to determine the variation in both breeding times and fitnesses among the males and females of the different phases. The results are used to test O'Donald's models of sexual selection. Models of specific mating preferences by which the males are sexually selected are also tested by fitting them to the distributions of breeding times of newly mated pairs.

2. THE ORIGIN OF THE FAIR ISLE DATA

The skuas on Fair Isle were first studied by K. Williamson when he became Warden of the Fair Isle Bird Observatory. Williamson (1965) gives a general account of Fair Isle and its birds. P. E. Davis, who became Warden in 1957, continued the study. From 1958 to 1960, he was assisted by P. O'Donald who was then a research student supported by a Nature Conservancy Studentship. O'Donald (1962) in his Ph.D. thesis analysed the data he had helped to collect and it was from these data that the fitness

function of breeding time, used in the computer models, was calculated (O'Donald, 1972*a*). R. J. Berry very generously made available to us his tabulation of all the original data from Fair Isle. The data were then coded for storage on a disk-file in the Titan Computer of the University of Cambridge.

3. THE FITNESS FUNCTION OF BREEDING TIME

In order to calculate the mean fitnesses of different phenotypes, which are determined by their different distributions of breeding times, the overall relationship between breeding time and fitness must be known. Table 1 shows the empirical relationship between the breeding time given by the

TABLE 1
Overall distribution of fitness in relation to breeding time

Breeding dates	No. of pairs fledging 0, 1 or 2 chicks			Mean fitness	Variance per pair
	0	1	2		
11-15	2	8	15	1.5200	0.40960
16	0	6	17	1.7391	0.19282
17	0	9	17	1.6538	0.22633
18	1	10	17	1.5714	0.31633
19	0	7	17	1.7083	0.20660
20	3	13	21	1.4865	0.41198
21	0	6	21	1.7778	0.17284
22	2	11	10	1.3478	0.40076
23	3	17	33	1.5660	0.35885
24	2	10	12	1.4167	0.40972
25	1	10	8	1.3684	0.33795
26	0	7	17	1.7083	0.20660
27-28	2	9	18	1.5517	0.38526
29-30	2	7	12	1.4762	0.43991
31-32	6	15	11	1.1562	0.50684
33-36	6	11	9	1.1154	0.56361
37-40	6	19	1	0.8077	0.23225
41-48	8	11	2	0.7143	0.39456
	44	186	258	1.4385	

number of days after the 1st of June when the first egg hatched and the fitness given by the average number of chicks fledged by pairs breeding at a given date. Hatching date is the most satisfactory measure of breeding time, for other possible measures like laying date are more difficult to determine accurately.

A quadratic equation can be fitted to data on breeding times and fitnesses as described by O'Donald (1972*a*). A convenient quadratic equation is

$$w = 1 - \alpha - K(\theta - x)^2$$

where w is the mean fitness of individuals breeding at time x . At $x = \theta$, w is at its maximum value of $1 - \alpha$. The mean and variance in fitness can be found in terms of parameters α , K and θ and the moments of the distribution of x . For relative fitnesses with a maximum at $w = 1$, we may put $\alpha = 0$ giving the relative fitness function

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

where $\phi = 1/K$. The mean relative fitness is therefore given by

$$\bar{w} = 1 - (\theta - \bar{x})^2 / \phi - V_x / \phi$$

where V_x is the variance of x . O'Donald (1972*a*) obtained the function $w = 1 - (0.473544 - x)^2 / 24.254$ for the relative fitness of pairs breeding in weekly intervals starting with the week 10-16 June. This function was used to calculate the sexual selective coefficients of the colour phases (O'Donald, 1972*c*). It fits the data given in table 1 very well: $\chi^2 = 2.38$ for 4 degrees of freedom.

Although the fitness function is a good fit to the overall data, there may be significant variations in fitness between pairs who have bred together for different numbers of years. The pairs can be classified by their breeding experience, given by the number of years they have previously bred together. It is clear from earlier work (O'Donald, 1962) that new pairs with no experience together breed much later on average than pairs who have several years of previous experience breeding together. The new pairs produce fewer offspring. This may be a result solely of their later breeding; or they may produce fewer offspring even when they breed at the same time as experienced pairs. If their reduced fitness is solely caused by their late breeding, then the overall fitness function can be used to calculate the coefficients of sexual selection operating on new pairs. If not, a separate fitness function valid for new pairs would have to be used.

In order to compare the fitnesses of pairs with different breeding experience, it is necessary to group the data into weekly intervals. Even so, there are hardly any individuals with several years' experience in the last interval. Table 2 shows the values of the fitness in those intervals in which there were enough pairs to provide reasonable estimates of fitness. When there were too few pairs of greater experience they were lumped with those of less experience as the table shows. The mean fitness in each interval is simply the mean number of chicks reared by the total number of pairs in each interval. Heterogeneity of fitness with experience is tested by χ^2 . Given the number of pairs of different experience in an interval, the number of chicks they are expected to produce can be calculated from the mean fitness of all pairs in the interval (assuming the null hypothesis that in a given interval there is no variation of fitness with experience). χ^2 cannot be calculated, however, by the simple formula

$$\chi^2 = \sum \frac{(\text{observed} - \text{expected nos.})^2}{\text{expected nos.}}$$

because each observed number of chicks is not a simple Poisson variate with a variance equal to the expected number. The variance is determined by the overall numbers of pairs who fledge zero, one or two chicks. Thus in any interval the fitness of individual pairs takes the values $w = 0, 1$ or 2 . If the proportions of pairs with these fitnesses are p, q and r (so that $p + q + r = 1$) then the variance in the fitness of a single pair can be calculated as follows:

$$\begin{array}{rcccl} \text{fitness, } w & 0 & 1 & 2 & \\ \text{proportion of pairs} & p & q & r & \\ \bar{w} & = & q + 2r & & \\ V_w & = & q + 4r - (q + 2r)^2 & & \\ & = & pq + 4pr + qr. & & \end{array}$$

TABLE 2
Fitness of pairs in relation to their breeding time and experience

Breeding dates in weekly intervals	Mean fitness in interval	Breeding experience given by no. of years pair previously bred together								Variance of one observation per pair	χ^2 for heterogeneity in interval	
		0	1	2	3	4	5	6	7			8+
1	1.6351	1.167	1.667	1.600	1.750	1.556	1.667	1.833	1.800	1.600	0.2858	6.80
2	1.5556	1.591	1.446	1.421	1.581	1.700	1.727	1.875	1.750	—	0.3488	9.43
3	1.5046	1.481	1.676	1.400	1.125	—	—	—	—	—	0.3601	6.53
4	1.0351	1.026	1.375	—	—	—	—	—	—	—	0.4900	2.95
5	0.8904	—	—	—	—	—	—	—	—	—	—	—

Summed for all weeks $\chi^2 = 25.71$ with 20 degrees of freedom. For this value of χ^2 , $0.1 < P < 0.2$.

Note that where values of fitness are missing, there were too few pairs to give reasonable values of χ^2 . Data of such pairs were lumped with those of the greatest breeding experience for which values are given. For example in week 3, pairs with more than 3 years' experience were all included with the pairs with 3 years' experience. Since pairs which hatched no eggs are excluded, the mean fitness in this table is higher than the mean fitness in tables 3 and 4 in which data from all pairs are included.

The values of the variance given in table 2 were calculated in this way. For n pairs the variance is $V_w = n(pq + 4pr + qr)$. Thus we calculate

$$\chi^2 = \Sigma \frac{(\text{observed} - \text{expected nos.})^2}{\text{variance}}$$

This calculation gives the values of χ^2 for heterogeneity shown in table 2. They are not significant.

4. THE COEFFICIENTS OF SEXUAL SELECTION

The data were analysed by computer to give the means and variances of breeding times and fitnesses in each of the phases and in different groupings of the phases in relation to breeding experience and sex. The results are shown in table 3 for males and in table 4 for females. The second column in the tables, headed "year", refers to the number of years pairs have been breeding together.

This analysis of breeding times is more detailed than Berry and Davis's analysis and more data are included, but the results are similar. In pairs breeding together for the first time, dark males breed on average before dark-intermediate males who breed before intermediate males who in turn breed before pale males. There is a similar sequence in the variances, the pale males being much the most variable in breeding time and the dark males the least variable. But these differences between the phases almost completely disappear in pairs breeding for 2 or more years together. And no such differences are found between phases in females. These facts strongly suggest that sexual selection favours the darker males. Sexual selection can only take place when pairs mate for the first time. If the females prefer the darker males or if the darker males compete more successfully for the females, then the distribution of breeding times of the darker males should have an earlier mean and a smaller variance than the distribution of the paler males. But these differences in the distributions of breeding times should disappear after the first year of breeding. Table 3 shows that there are no significant differences in the means and variances of the breeding times of the phases after the first year.

Given the means and variances of the breeding times, the fitnesses of the different phases can be calculated from the fitness function. Thus O'Donald (1972*c*) obtained the following values of the sexual selective coefficients measuring the relative disadvantage of intermediate and pale males:

$$s_I = 0.13$$

$$s_P = 0.34$$

From the data given in this paper, the sexual selective coefficients can be calculated directly from the empirical fitnesses given in table 1. The breeding times of new pairs of males are shown in fig. 1. The fitnesses of these pairs taken from table 1 give the average fitnesses of the different phases of males in new pairs. For pale males $w_P = 1.0980$; for intermediate and dark-intermediate males $\bar{w}_I = 1.2641$; and for dark males $\bar{w}_D = 1.3635$. The sexual selective coefficients are therefore:

$$s_I = 0.0729$$

$$s_P = 0.195.$$

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TABLE 3

Males

Type	Year	No.	Breeding date		No.	No. chicks fledged	
			Mean	Variance		Mean	Variance
P	1	26	33.923	90.554	37	0.703	0.604
P	2	16	25.062	17.796	22	1.091	0.753
P	3	11	22.818	24.364	13	1.385	0.423
P	4	8	20.875	25.268	11	1.091	0.691
P	5	4	24.250	8.250	4	2.000	0
P	6	4	22.500	25.667	4	1.750	0.250
P	7	3	24.000	39.000	3	1.667	0.333
P	8	2	20.500	24.500	3	2.000	0
P	9	2	18.500	4.500	3	1.333	1.333
P	10	1	18.000	0	2	1.500	0.500
NOTP	1	146	29.062	56.803	211	0.948	0.688
NOTP	2	94	24.383	32.949	116	1.310	0.581
NOTP	3	58	22.845	27.572	73	1.315	0.413
NOTP	4	41	20.610	19.094	46	1.435	0.473
NOTP	5	24	19.167	20.667	30	1.400	0.524
NOTP	6	19	18.105	15.544	20	1.550	0.471
NOTP	7	9	18.222	6.944	12	1.750	0.386
NOTP	8	5	16.600	9.300	7	1.429	0.619
NOTP	9	2	12.500	4.500	3	1.667	0.333
NOTP	10	1	16.000	0	1	1.000	0
I	1	57	30.614	59.170	90	0.811	0.672
I	2	36	26.611	36.359	48	1.083	0.674
I	3	26	23.615	19.286	29	1.310	0.436
I	4	15	22.933	24.352	17	1.235	0.691
I	5	10	21.200	32.622	12	1.417	0.811
I	6	7	18.143	6.143	7	2.000	0
I	7	3	18.333	8.333	4	1.750	0.250
I	8	2	19.000	18.000	3	1.667	0.333
I	9	0	0	0	1	1.000	0
I	10	1	16.000	0	1	1.000	0
I & DI	1	92	29.707	62.034	134	0.873	0.668
I & DI	2	54	25.463	36.442	68	1.279	0.622
I & DI	3	35	23.371	24.711	40	1.300	0.421
I & DI	4	23	21.739	23.202	26	1.346	0.555
I & DI	5	14	20.286	25.912	17	1.294	0.721
I & DI	6	9	17.556	6.028	9	1.778	0.194
I & DI	7	5	17.400	5.800	6	1.833	0.167
I & DI	8	3	17.667	14.333	5	1.400	0.800
I & DI	9	0	0	0	1	1.000	0
I & DI	10	1	16.000	0	1	1.000	0
DI	1	30	28.700	64.631	37	1.027	0.694
DI	2	14	24.571	29.956	15	1.800	0.171
DI	3	6	24.667	54.267	7	1.000	0.333
DI	4	5	20.800	16.700	6	1.333	0.267
DI	5	3	18.667	4.333	4	1.000	0.667
DI	6	1	15.000	0	1	1.000	0
DI	7	1	16.000	0	1	2.000	0
DI	8	0	0	0	1	0	0
DI	9	0	0	0	0	0	0
DI	10	0	0	0	0	0	0

TABLE 3 (continued)

Type	Year	No.	Breeding date		No.	No. chicks fledged	
			Mean	Variance		Mean	Variance
DI & D	1	70	28.471	53.180	96	1.073	0.679
DI & D	2	42	22.929	23.044	50	1.520	0.459
DI & D	3	22	22.136	28.314	30	1.300	0.355
DI & D	4	20	19.500	12.158	22	1.545	0.260
DI & D	5	12	18.083	8.992	15	1.467	0.410
DI & D	6	10	18.000	25.556	11	1.273	0.618
DI & D	7	4	18.500	11.000	6	1.667	0.667
DI & D	8	2	15.000	0	3	1.000	1.000
DI & D	9	2	12.500	4.500	2	2.000	0
DI & D	10	0	0	0	0	0	0
D	1	39	27.974	42.815	56	1.107	0.679
D	2	28	22.107	18.470	33	1.455	0.506
D	3	15	20.867	17.552	22	1.364	0.338
D	4	14	19.000	11.692	15	1.667	0.238
D	5	8	17.625	11.982	10	1.700	0.233
D	6	8	17.750	27.929	9	1.222	0.694
D	7	2	17.500	4.500	4	1.500	1.000
D	8	2	15.000	0	2	1.500	0.500
D	9	2	12.500	4.500	2	2.000	0
D	10	0	0	0	0	0	0

These values are lower than those calculated by the fitness function but the differences are not statistically significant. They are not true selective coefficients, however, for they apply only to new pairs, which make up 36 per cent of all pairs. The mean selective coefficients resulting from the variation in fitness at breeding time are therefore:

$$s_I = 0.026$$

$$s_P = 0.070.$$

These are the coefficients of sexual selection.

The overall differences in fitness between the phases can be calculated empirically. Tables 3 and 4 give a complete analysis of fitness by phase, sex and breeding experience. The mean fitnesses averaged over pairs with different breeding experience are shown in table 5. Most of the variation in fitness in the males comes from the new pairs and a considerable part of their variation in fitness is caused by their variation in breeding time and hence by sexual selection.

An analysis of variance of the differences in fitness can be carried out treating the pairs with different breeding experience as "blocks" in a randomised block experiment. For males we get the following mean squares (M.S.):

$$\begin{aligned} \text{M.S. (between phases)} &= 2.6538 \\ \text{M.S. (within phases and experience)} &= 0.5774. \end{aligned}$$

The variance ratio is $F = 4.60$ which is significant at a probability of $P = 0.01$. For females we obtain:

$$\begin{aligned} \text{M.S. (between phases)} &= 0.6900 \\ \text{M.S. (within phases and experience)} &= 0.5730 \end{aligned}$$

and the variance ratio is not significant.

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TABLE 4

Females

Type	Year	No.	Breeding date		No.	No. chicks fledged	
			Mean	Variance		Mean	Variance
P	1	34	31.471	61.105	52	0.692	0.609
P	2	28	24.536	26.480	33	1.303	0.655
P	3	13	22.462	19.936	18	1.278	0.448
P	4	13	19.615	19.423	14	1.643	0.401
P	5	5	20.000	22.500	7	1.429	0.952
P	6	6	18.833	31.767	6	1.500	0.300
P	7	4	20.500	53.667	5	1.400	0.800
P	8	1	16.000	0	2	2.000	0
P	9	0	0	0	2	0.500	0.500
P	10	1	16.000		1	1.000	0
NOTP	1	139	29.345	64.605	197	0.970	0.683
NOTP	2	82	24.463	32.375	105	1.267	0.601
NOTP	3	56	22.929	28.613	68	1.338	0.406
NOTP	4	36	21.028	19.685	43	1.279	0.539
NOTP	5	23	19.870	22.664	27	1.481	0.413
NOTP	6	17	18.882	16.360	18	1.611	0.487
NOTP	7	8	19.250	6.214	10	1.900	0.100
NOTP	8	6	18.000	16.000	8	1.500	0.571
NOTP	9	4	15.500	15.000	4	2.000	0
NOTP	10	1	18.000	0	2	1.500	0.500
I	1	74	29.689	65.779	104	0.990	0.709
I	2	39	24.359	26.236	51	1.294	0.652
I	3	29	23.966	29.820	34	1.382	0.365
I	4	16	20.500	17.333	19	1.316	0.561
I	5	7	18.714	20.571	10	1.400	0.489
I	6	5	18.800	10.700	5	2.000	0
I	7	3	21.333	4.333	3	1.667	0.333
I	8	2	16.000	2.000	2	1.500	0.500
I	9	2	15.500	4.500	2	2.000	0
I	10	0	0	0	1	1.000	0
I & DI	1	101	29.099	66.510	141	0.965	0.677
I & DI	2	54	23.704	28.401	71	1.338	0.656
I & DI	3	39	22.923	28.231	46	1.413	0.337
I & DI	4	24	20.292	14.303	30	1.333	0.575
I & DI	5	12	18.417	19.174	16	1.438	0.396
I & DI	6	10	17.900	8.544	10	1.900	0.100
I & DI	7	5	19.800	7.700	6	1.833	0.167
I & DI	8	5	17.200	15.200	5	1.800	0.200
I & DI	9	4	15.500	15.000	4	2.000	0
I & DI	10	1	18.000	0	2	1.500	0.500
DI	1	20	28.250	75.461	29	0.828	0.576
DI	2	9	22.222	37.444	13	1.538	0.603
DI	3	9	20.222	13.194	9	1.444	0.278
DI	4	5	20.800	6.700	8	1.125	0.696
DI	5	3	16.667	20.333	4	1.500	0.333
DI	6	3	16.000	3.000	3	2.000	0
DI	7	0	0	0	1	2.000	0
DI	8	1	15.000	0	1	2.000	0
DI	9	1	11.000	0	1	2.000	0
DI	10	0	0	0	0	0	0

TABLE 4 (continued)

Type	Year	No.	Breeding date		No.	No. chicks fledged	
			Mean	Variance		Mean	Variance
DI & D	1	44	30.205	67.701	67	0.925	0.646
DI & D	2	26	24.962	40.438	35	1.257	0.550
DI & D	3	20	21.000	12.632	22	1.318	0.418
DI & D	4	15	22.067	24.638	18	1.167	0.500
DI & D	5	13	20.846	24.808	14	1.571	0.418
DI & D	6	9	18.778	25.194	10	1.400	0.711
DI & D	7	2	18.000	8.000	4	2.000	0
DI & D	8	2	18.500	24.500	4	1.250	0.917
DI & D	9	1	11.000	0	1	2.000	0
DI & D	10	0	0	0	0	0	0
D	1	22	31.227	58.470	35	1.029	0.734
D	2	17	26.412	38.007	20	1.050	0.471
D	3	11	21.636	12.455	13	1.231	0.526
D	4	10	22.700	34.011	10	1.200	0.400
D	5	10	22.100	20.989	10	1.600	0.489
D	6	6	28.167	32.167	7	1.143	0.810
D	7	2	18.000	8.000	3	2.000	0
D	8	1	22.000	0	3	1.000	1.000
D	9	0	0	0	0	0	0
D	10	0	0	0	0	0	0

TABLE 5

Mean fitnesses of the phases in males and females

	Males		Females	
	Fitness	Selective coefficient	Fitness	Selective coefficient
Dark	1.3465	0	1.1685	0
Intermediate and dark-intermediate	1.1366	0.156	1.2358	-0.0576
Pale	1.1080	0.177	1.1214	0.0403

5. MATING PREFERENCES FOR THE PHASES

The selective differences we have demonstrated to exist between the phases of males are determined by the number of offspring the different pairs succeed in fledging. A considerable component of the selection depends on the breeding times of new pairs. This may be defined as sexual selection because it is caused by mating behaviour and not by fertility or the chances of survival. The mechanism which causes the variation in the chances of mating during the breeding season is not of course known. The females may have preferences for mating with dark or intermediate males caused by differences in the males' mating behaviour; or the males may compete with each other through their threat displays. Models of sexual selection are more easily described in terms of mating preferences while being valid for selection by direct competition between males. Mating preferences provide the more likely mechanism, however, and we shall describe four specific models, in these terms.

The models are used to predict the distributions of breeding times of the phases of males, dark, intermediate (including dark-intermediate) and pale, in new pairs. Fig. 1 and 2 show the actual distributions of males in new pairs and in pairs with 2 or more years of previous breeding experience. The

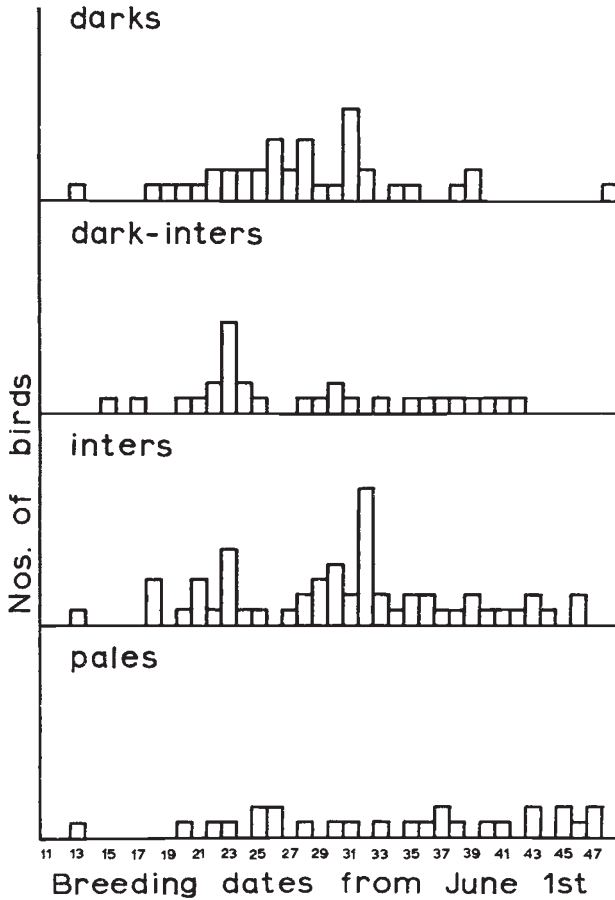


FIG. 1.—The distributions of breeding times of the different phases of males in pairs who are breeding together for the first time.

data from different years have been adjusted to a common median, but this adjustment has only a slight effect. As table 3 proves, in new pairs, pales have a much later mean breeding time with a higher variance than intermediates and darks. But the difference almost disappears with more breeding experience. In fitting the models to the distributions, the breeding times were grouped into weekly intervals as shown in table 6.

Model 1. This model has already been described in detail by O'Donald (1973a). It was the model which showed that sexual selection in monogamous birds is necessarily frequency-dependent (O'Donald, 1972b, 1973a). It assumes that there are two phenotypes of male. Some females, who represent a proportion α of all females, have a mating preference for one of the male phenotypes. They always mate with the preferred males if they

can, but they will mate with the other males if none of their preferred males are available. The remaining females, a proportion $1 - \alpha$ of the total, then mate at random with the two male phenotypes. In a given interval of time, i , in the breeding season, there is assumed to be a proportion p_i of females

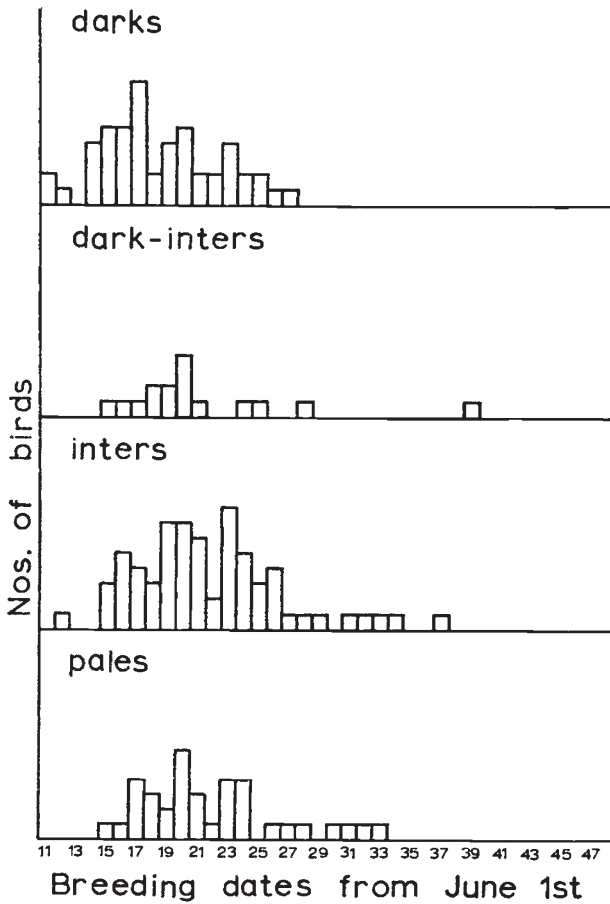


FIG. 2.—The distribution of breeding times of the different phases of males in pairs who have bred together at least 2 years previously.

TABLE 6
Distributions of breeding times of colour phases of males grouped in weekly intervals

Breeding dates in weekly intervals	Numbers breeding in interval			Total
	Pales	Intermediates and dark-intermediates	Darks	
10-16 June	1	2	1	4
17-23 June	3	24	8	35
24-30 June	6	19	16	41
1-7 July	6	24	10	40
8-14 July	5	15	3	23
15-21 July	5	2	1	8
Total	26	86	39	151

who are ready to mate: αp_i mate with the preferred males and $p_i(1-\alpha)$ mate at random among the males who are then still unmated. The weekly intervals given in table 6 were used in the computer program (details given in O'Donald, 1973a) to simulate the actual numbers of the different phases of males. The proportions, p_i , of females breeding in the weekly intervals were obtained from the weekly totals: the numbers of the different phases simulated in the computer for each weekly interval necessarily add up to the weekly totals in table 6. The marginal totals are therefore fixed: this is so for all the models.

Model 1 assumes that dark and intermediate males are equally desirable: darks and intermediates were added together to form a class of not-pale males phenotypically preferred as mates to the pales. Table 6 thus becomes a table of 2×6 values. χ^2 was calculated for values of α from $\alpha = 0.01$ by steps of 0.01 up to $\alpha = 1.0$. Minimum χ^2 was obtained at $\alpha = 0.52$ when $\chi^2_{\min} = 0.8846$. Since the marginal totals were fixed, 7 degrees of freedom were lost, and an additional degree of freedom was also lost by lumping the numbers in the first and second week. Thus 4 degrees of freedom were left. However, because the numbers of degrees of freedom are greater for the other models, we decided to use χ^2 as an approximation to the log likelihood and obtain the 2-unit support limits of the log likelihood. The log likelihood is defined as:

$$\log L = \sum a \log_e m$$

where the values of a are the observed numbers in the classes with expected numbers m . Approximately

$$\sum a \log_e m = \text{constant} - \frac{1}{2}\chi^2$$

If we subtract $\frac{1}{2}\chi^2_{\min}$ from the values of $\frac{1}{2}\chi^2$ obtained for the other values of α , the particular values for which $\frac{1}{2}\chi^2 - \frac{1}{2}\chi^2_{\min} = 2$ will then be the approximate 2-unit support limits of α (Edwards, 1972). These are the values $\alpha = 0.25$ and $\alpha = 0.65$. It would have been better to calculate the log likelihoods directly, but since this was not done in the original calculations the approximation by χ^2 was used instead.

Model 2. Like model 1, this model uses a single parameter α for the proportion of females who have a mating preference. However the females with the preference mate first with dark males; if there are no darks left, they then mate with intermediates, and finally if no intermediates are left either, they mate with pales. The remaining $1-\alpha$ of the females mate at random among remaining unmated males. The minimum χ^2 of 12.16 occurs at $\alpha = 0.12$. The observed numbers were grouped into 13 classes from which 7 degrees of freedom have been lost. The minimum χ^2 with 6 degrees of freedom is not quite significant representing a probability of $P = 0.06$. However the values of χ^2 are all well outside the approximate 2-unit support limits given by the other models. Model 2 is therefore much the least likely of the four models.

Model 3. In this model a proportion α of the females prefers only darks and mates at random with the other phases if there are no darks left to mate with. Another proportion β prefers both darks and intermediates. The α females have the first choice of the available males in each weekly interval of the breeding season. The β females then mate at random between the intermediate males and the remaining dark males, and they mate with pales

when there are no other phases left unmated. The $1 - \alpha - \beta$ of the rest of the females mate at random between all phases. This model thus becomes the same as model 1 when $\alpha = 0$. χ^2 has 6 degrees of freedom compared to 4 in model 1. However, when $\alpha = 0$, the 2-unit support limits of β are $\beta = 0.25$ and $\beta = 0.65$ —the same limits as those for α obtained from model 1. $\chi^2_{\min} = 4.680$ when $\alpha = 0.08$ and $\beta = 0.40$.

Model 4. In model 4, proportions α , β and γ of the females prefer dark, intermediate and pale males respectively. Without any of their preferred males to mate with, they mate at random. The remaining $1 - \alpha - \beta - \gamma$ of the females mate at random with all phases. O'Donald (1973*b*) has given the results of computer simulations of the rate of selection using this model. If the three phases are genetically determined by two alleles so that the dark and pale phases are the two homozygotes and the intermediates are the heterozygotes, then the computer simulations show that a stable equilibrium is reached when the frequency of the dark allele is approximately

$$p_e = \frac{\alpha + \frac{1}{2}\beta}{\alpha + \beta + \gamma}$$

There is indeed clear evidence that the pales are pure breeding and therefore homozygous, but intermediates and darks may be misclassified as heterozygotes and homozygotes (O'Donald and Davis, 1959). During the course of selection in model 4, the favoured allele starts with a selective advantage that is more or less additive, the heterozygote being at less of an advantage than the favoured homozygote. But as equilibrium is approached, the overall advantage passes to the heterozygote and maintains the equilibrium. In all the other models, the favoured allele spreads through the population to complete fixation.

In using model 4 to simulate the distributions of breeding times it was assumed that $\gamma = 0$. Then $\chi^2_{\min} = 4.375$ at the point $\alpha = 0.18$ $\beta = 0.29$ which gives an equilibrium gene frequency of $p_e = 0.68$. The minimum χ^2 is slightly smaller for this model than for model 3: model 4 is therefore the model with the greatest likelihood. In both models the 2-unit support limits of the total mating preference $\theta = \alpha + \beta$ are $0.18 < \theta < 0.67$. For model 4, the support limits for β in relation to given values of α give the overall support limits of the equilibrium gene frequency in a range of values $0.832 \geq p_e \geq 0.625$. The actual gene frequency of the dark allele is lower than this. It varies between males and females and is slightly higher in males as we should expect if the theory is true. And it can be estimated in two ways. We can assume that darks and pales are both homozygous and find the total proportion of dark alleles, or we can assume that the genotypes are approximately in the Hardy-Weinberg proportions and calculate the frequency of the pale allele from the proportion of pale phenotypes. The frequencies in females give the following estimates:

$$\begin{aligned} p_{\text{f}} &= 0.475 \text{ (assuming darks and pales are homozygous)} \\ p_{\text{f}} &= 0.518 \text{ (by Hardy-Weinberg Law).} \end{aligned}$$

In males the corresponding estimates are:

$$\begin{aligned} p_{\text{m}} &= 0.558 \text{ (darks and pales homozygous)} \\ p_{\text{m}} &= 0.586 \text{ (Hardy-Weinberg Law).} \end{aligned}$$

These estimates were obtained from the numbers of different individuals in the skua colony. There are no significant differences in gene frequency in individuals with different breeding experience.

The gene frequencies do not lie in the range of equilibrium values predicted by model 4. However in the Fair Isle population, equilibrium might not have been reached: the darks may still have been increasing in frequency as a result of selection. Any selective changes are certain to be slow from one year to the next for adult skuas live a long time: a generation may be as long as 10 years. This would explain why the frequencies of the phases remained more or less constant in the 14 years that the colony was

TABLE 7
Relative survival of colour phases from one breeding season to the next

Phase	Females		Males		Both sexes		Variance $p(1-p)$	χ_1^2
	Probability of survival p_f	No. n_f	Probability of survival p_m	No. n_m	Probability of survival p	No. n		
Darks	0.7391	46	0.8585	106	0.8224	152	0.1461	3.13
Intermediates and dark-intermediates	0.7857	224	0.7978	183	0.7912	407	0.1652	0.09
Pales	0.8202	89	0.7755	49	0.8043	138	0.1574	0.40
Total	0.7883	359	0.8136	338	0.8006	697	0.1597	0.70

For each phase χ_1^2 is calculated by the formula

$$\chi_1^2 = \frac{(p_f - p)^2}{\left(\frac{p(1-p)}{n_f}\right)} + \frac{(p_m - p)^2}{\left(\frac{p(1-p)}{n_m}\right)}.$$

The heterogeneity in mortality in phases of different sex is given by

$$\chi_2^2 = 2.92.$$

studied. At the same time it is possible that natural selection resulting from differences in mortality between the phases maintains the equilibrium at its present frequency by opposing the sexual selection. As O'Donald (1973a) has shown, such equilibria are stable provided the mating preferences are not shared by more than 40-45 per cent of the females. An equilibrium maintained by the opposing forces of natural and sexual selection is stable only if the sexual selection is negatively frequency dependent. This is true of mating preferences involving no more than about 45 per cent of females. In both models 3 and 4, mating preferences involving only 19 per cent of the females are allowable within the 2-unit support limits. There is evidence given in table 7 of differences in mortality between the phases but the numbers of individuals are too few for the differences to be significant. If they were significant, the differences in mortality would certainly give rise to natural selection that could balance the sexual selection at a point of stable equilibrium.

The four models compared. As we have shown, model 2 is the least likely, while model 4 is slightly more likely than model 3. Model 2 can certainly be rejected in comparison with the others because all its values of χ^2 lie well outside the 2-unit support limits of models 3 and 4. Fig. 3 shows these approximate support limits, together with the point of maximum likelihood

for each model. By collecting more data on the Arctic skuas of Fair Isle, we hope to obtain a closer set of limits that will permit more precise predictions to be made for comparison with the observations.

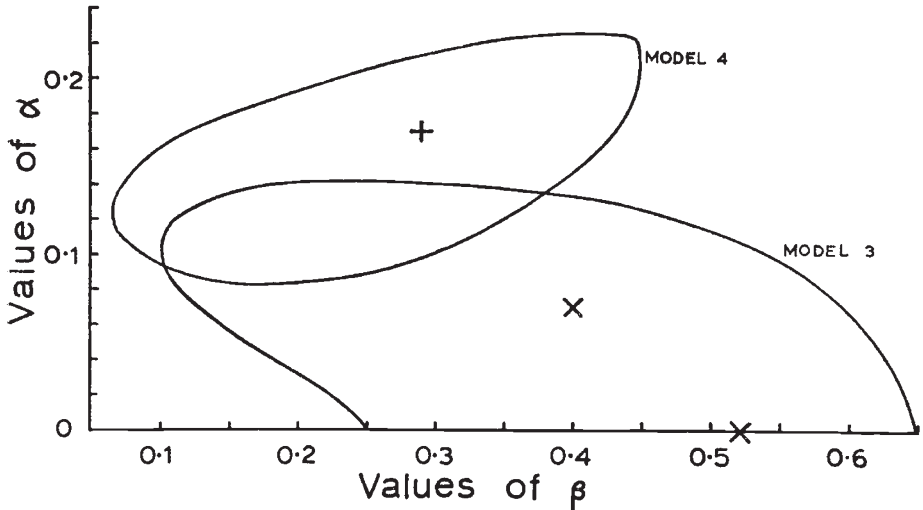


FIG. 3.—The approximate support limits of female mating preferences for models 3 and 4. Values of α and β lying inside the closed areas are within the 2-unit support limits. The symbol “+” marks the point of minimum χ^2 in model 4. The symbols “x” mark the points of minimum χ^2 in model 3 when $\alpha > 0$ and $\alpha = 0$.

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