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MATING PREFERENCES AND SEXUAL SELECTION IN THE ARCTIC SKUA

II. BEHAVIOURAL MECHANISMS OF THE MATING PREFERENCES

P. O'DONALD

Department of Genetics, University of Cambridge, Downing Street, Cambridge CB2 3EH, England

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SUMMARY

Models of female mating preferences in birds can be derived on the assumption that females have certain thresholds in their receptivity to male courtship that must be exceeded before they mate. In one group of models, the males vary in gonadotrophin and androgen level. Males with higher levels of these hormones maintain larger territories and court females more actively and persistently. They will be more likely to obtain a response from females with high thresholds who require a lengthy period of courtship before mating. In other models, territory size directly determines mating success. Males with larger territories occupy more of the breeding ground. If females land at random on the breeding ground, they will land more often on the larger territories. Males with larger territories thus have increased opportunities for mating. In a third group of models, some females have a lower threshold of response to males with particular characteristics who thus gain an advantage since the females respond to them more quickly. These models of mating behaviour would explain the mating preferences that act in favour of melanic Arctic Skuas. Observations on the behaviour during pairing provide support for some models and refute others. In the model that gives the best fit to the data, many females have a lower threshold of response towards either the dark or the intermediate males. These males find mates before the others and gain an advantage from increased reproductive success. Further observations are required to discriminate between models that depend on variation in male courtship and models that depend on variation in female response.

1. INTRODUCTION

IN the first paper of this series, O'Donald, Wedd and Davis (1974) analysed data on breeding date and reproductive success in a polymorphic population of a seabird, the Arctic Skua, on the island of Fair Isle in Shetland. The three phenotypes, dark, intermediate and pale correspond roughly to three genotypes determined by two alleles, but with some overlap and misclassification of intermediate and dark. Sexual selection favours the melanic, dark and intermediate males: on average they breed before the non-melanic, pale males when pairing with a new female, thus gaining an advantage because early breeding increases reproductive success. O'Donald, Wedd and Davis suggested that females prefer to mate with melanic males: this would increase the melanics' chance of mating so they would usually have paired before the pales. The difference in breeding dates is observed only when new pairs are being formed: it disappears in later years if the males continue to breed with the same females. No differences in breeding dates are observed between the females.

O'Donald (1973, 1974) analysed the genetic consequences of sexual selection in which an advantage is gained by breeding early in the breeding season. In computer models, the males are ready to mate at the start of the breeding season. They defend their territories on the breeding grounds. The females become ready to mate during successive intervals in the breeding season. Those females that prefer particular phenotypes of males mate with any of the unmated males of their choice. The remaining females then mate at random with the remaining unmated males. Females with preferences also mate at random if none of the preferred males remain unmated. Thus the matings take place among groups of males and females with preferential matings preceding random matings. In fitting the models to data on the Arctic Skua, the actual distribution of the breeding dates was arbitrarily divided into weeks corresponding to the intervals in which the females are assumed to reach breeding condition. The models were then used to compute the proportions of pale, intermediate and dark males breeding in each interval. The fitness function of breeding at a given date then determines the average fitness of the male genotypes and their sexual selective coefficients.

O'Donald, Wedd and Davis (1974) generalised these models in the following ways.

(i) In model 1, a proportion α of the females prefer darks and intermediates indiscriminately.
(ii) In model 2, α of the females prefer darks rather than intermediates or pales, but prefer intermediates rather than pales if no darks are left unmated.
(iii) In model 3, α of the females prefer darks and β prefer darks and intermediates indiscriminately.
(iv) In model 4, α of the females prefer darks and β prefer intermediates.

The models were used to estimate the parameters, α and β, of the mating preferences. Later O'Donald (1976) generalised these models further. The preferential matings were allowed either to precede (P models) or to follow (R models) the random matings. Lower levels of mating preferences fit the Arctic Skua data if random matings come first. If the females arrive singly and successively to breed, both the P and R models then become identical: they are equivalent to models in which preferential and random matings occur simultaneously (S models). These P, R and S models were programmed for each of the models, 1 to 4, of the mating preferences. By fitting these models to the data, O'Donald (1976) found that model 4 had a slightly higher likelihood than the others and the R models had slightly higher likelihoods than the P and S models: model 4R was found to be the model with the highest likelihood of all. However, except for model 2, which the data clearly refuted, the likelihoods of all the other models were close indeed and in no way discriminated between the models.

The Arctic Skuas of Fair Isle have been studied from 1948 to 1962, and from 1973 to 1976. The population has continually increased in size and now consists of 140 pairs of breeding birds. In the following paper of this series, O'Donald and Davis (1977) include all the data collected up to 1976, obtaining more accurate estimates of the mating preferences and testing the residual heterogeneity after fitting the models. In the present paper, I discuss behavioural mechanisms that may determine a male's chances of mating and relate these mechanisms to our models of mating preference. Variation in the males' chances of mating may be determined in two different ways: the males may vary in competitive ability with other males or in the level and persistence of their courtship activity; the females may vary in their responses to different male phenotypes.

2. VARIATION IN MALE COURTSHIP

A male may gain a direct mating advantage by increasing the intensity and persistence of his sexual behaviour. His aggressive and territorial behaviour may be more intense. If a male successfully defends a larger territory, occupying more of the breeding area, the sexual opportunities of other males will be reduced. I shall show in section 3 that territory size may directly determine mating success. Males may also vary in their ability to attract females as a result of variation in the frequency and intensity of their courtship activities. Aggressive behaviour and courtship behaviour are closely related. Levels of gonadotrophin and androgen determine both types of behaviour (see below). A male that is more aggressive at the beginning of the breeding season, driving off other males and maintaining a larger territory, may also show more intense courtship behaviour later in the season. Mating success will therefore increase for both reasons. Watson and Moss (1971) found that when unsuccessful male red grouse were implanted with androgen, they greatly increased both their territory size and mating success. Witschi (1961) reviewed evidence showing that androgen level was directly correlated with aggressiveness and the development of combs and wattles in poultry, singing in canaries, nest building behaviour in Black-browed Herons and generally with nuptial plumage in many sexually dimorphic birds.

In pigeons, Murton, Westwood, and Thearle (1973) found that the melanic, blue-checker and dark-blue-checker males have larger testes and higher sperm counts than the non-melanic, wild-type males. The melanics show an earlier recrudescence of the gonads and their gonads are less likely to regress in the autumn: they have a different photoperiod and a longer breeding season. This presumably gives them an advantage in the urban environments where melanic pigeons are found: sufficient food may be available for breeding throughout the year. The melanic pigeons also have a mating advantage. Davis and O'Donald (1976*a*) found that a model of negative assortative mating gave a good fit to Murton, Westwood and Thearle's data of the numbers of the different matings between the various melanic and non-melanic phenotypes. Maximum likelihood estimation of the mating preferences showed no preferences for wild-type, while about 51 per cent prefer blue-checker and 38 per cent prefer dark-blue-checker.

A similar physiological affect may thus determine the sexual advantage of the melanic Arctic Skuas. Higher levels of gonadotrophin and androgen may be responsible for their increased mating success. There is some evidence, which does not, however, reach the 5 per cent level of statistical significance, that the melanic males have larger territories (see Section 3). A difference in gonadotrophin and androgen level would provide the simplest and most direct explanation of the difference in territory size. Unlike the pigeons, however, melanic and non-melanic skuas do not differ in the length of their breeding season. Presumably, they do not differ in their photoperiods.

Male courtship must be specific and at a certain level of intensity to elicit a response from the females: a certain threshold must be reached before the female will mate. If females vary in the threshold at which they will respond, some will require longer periods of courtship than others. If a certain amount of stimulation is necessary to exceed a female's threshold and elicit her mating response, a sexually more active male will produce the necessary stimulation in a shorter period of time than a less active male. The higher the threshold, the greater will be the difference in the time required for more active and less active males to get a response: at high thresholds, the more active males will get a response a long time before the less active males do so; at low thresholds, both males may get responses almost equally quickly. Thus, in a group of females in breeding condition, random matings will tend to take place first, followed by preferential matings.

If groups of females come into breeding condition in successive intervals of the breeding season, this mechanism of pairing may produce a result described by the R models (O'Donald, 1976; O'Donald and Davis, 1977): a proportion of the females in a particular interval in the breeding season pair at random with the melanic and non-melanic males; the preferential matings of the females with higher thresholds of response then follow the random matings.

This model of mating behaviour will often be too simple, however: female response is likely to be a continuous variable in which a certain proportion of females would have thresholds low enough for both types of male to elicit a quick response. The remaining females would then respond later and, on average, more readily with the melanic than with the non-melanic males. Matings of melanic males would take place preferentially but to some extent simultaneously with matings of non-melanic males. A more realistic model would therefore combine both R and S models. A combined model would be easy to set up, but the present data are insufficient to make this worthwhile.

3. Variation in territory size

A male with higher levels of gonadotrophin and androgen is probably more aggressive towards other males, as well as being sexually a more desirable mate. He may thus gain an additional advantage by restricting the other males' chances of mating. If he maintains a larger territory, his chances of encountering females will increase in direct proportion to the increased territory size. Mating success should therefore be proportional to territory size: if the females land at random on the breeding grounds, they will be more likely to land on the larger territories. Males with larger territories will generally find mates sooner than those with smaller territories. This should therefore produce a correlation between territory size and breeding time, earlier pairs having larger territories. Davis and O'Donald (1976*a*) observed that males with larger territories who have paired with a new female breed earlier in the season. The correlation is greatest among males who have bred in previous years and who have changed mates. There is no correlation among males breeding with the same female in subsequent years. O'Donald (1977) constructed a theoretical model of the relationship between territory size and breeding time with the following symbols.

p_{ij} is the probability that the jth male is unmated when the ith female arrives ($p_{1j} = 1$).
$p_{i+1,j}$ is the probability that the jth male is unmated when the $(i+1)$th female arrives.
P_{ij} is the probability that the jth male mates with the ith female.
x_j is the size of the jth male's territory.

The probability that the ith female mates with the jth male is then assumed to be proportional to the size of the territory and the probability that the male is still unmated. Thus we calculate

$$P_{ij} = (p_{ij}x_j)/(\sum_j p_{ij}x_j)$$

If $P_{ij} < p_{ij}$ then we put $P_{i+1,j} = p_{ij} - P_{ij}$ or if $P_{ij} > p_{ij}$ then we put $P_{ij} = p_{ij}$ and $P_{i+1,i} = 0$. The values of P_{ij} can thus be calculated in a computer, given the values of the territory size of the males. The matrix of values, P_{ij}, is the bivariate probability density of territory size and breeding date. If b_i is the breeding date of the ith female the hypothetical correlation of territory size and breeding date can then be found. O'Donald (1977) showed that this will give rise to selection for increased territory size because earlier pairs have greater success in fledging chicks (O'Donald, 1972).

Davis and O'Donald's data (1976*a*) fit the theory very well. When males with previous breeding experience pair with a new female, the observed correlation between territory size and breeding time is $r = -0{\cdot}462$. The hypothetical correlation, given observed territory sizes and breeding times, is $r = -0{\cdot}394$. The actual regression of breeding date on territory size is $b = 35{\cdot}51 - 0{\cdot}01704x$ compared to the hypothetical regression $b = 34{\cdot}45 - 0{\cdot}01454x$.

Fig. 1 in Davis and O'Donald's paper (1976*a*) shows the phenotypes of the males in addition to their breeding date and territory size. The pale males generally have the smaller territories and later breeding dates than the intermediate and dark males. However, there are only seven pale males in the sample and their mean territory size does not differ significantly from the rest. If this difference were a real one, it would certainly be sufficient to explain the differences in the breeding times of males who are pairing with new females, and hence the sexual selection in favour of the melanic males. From the observed territory sizes of the different males, the breeding dates of the females and the hypothetical bivariate frequency density, P_{ij}, we can find the average breeding date of each male phenotype. These values can then be compared with the actual mean breeding dates of males who have paired with a new female. The table shows the results of these calculations.

Although the hypothesis so closely agrees with the facts, territory size is unlikely to be the direct cause of mating success in the Arctic Skua. Invariably, when males change their mates, they remain on their territories of previous years. Their new mate is often a female who bred nearby in the past. Females do not therefore land at random on the breeding grounds, as the theory assumes. Even if they are mating for the first time, it is unlikely that the females distribute themselves at random over the breeding grounds. On the contrary, from observations of behaviour, the young birds are seen to congregate together in groups, called " clubs ", in particular parts of the Arctic Skua colony. They appear to form pairs in these clubs in the years before they actually breed. The greatest differences between the phenotypes in their breeding date and breeding success are observed in the first year of breeding and yet the males do not appear to defend territories in the clubs in which most of the sexual selection probably takes place. The relationship between territory size and breeding time may be the effect of the increased mating success of melanic males rather than the direct cause of it. Alternatively, territory size may have no relationship with melanism at all, since the difference in territory size between melanic and non-melanic males is not statistically significant in the small samples obtained so far.

TABLE

Comparison of observed breeding dates with hypothetical breeding dates if a male's chances of mating depends on his territory size

Male phenotype	Mean breeding date (measured in days from June 1st)	
	Observed	Hypothetical
Pale	34·09	33·78
Intermediate	30·05	29·84
Dark	29·22	29·70

The hypothetical breeding dates have been calculated using the observed distribution of breeding times and the hypothetical bivariate distribution of territory size and breeding date. The hypothetical values are very close to the observed values. The observed differences in territory size from which the hypothetical values were calculated are not significant. The differences in the observed breeding dates are very significant, however, having been calculated from large samples.

4. VARIATION IN FEMALE RESPONSE

Females may respond differently to the different male phenotypes. There is good evidence in fowls that the females of different breeds respond to different visual stimuli (Lill and Wood-Gush, 1965). For example, if female Arctic Skuas responded at different thresholds to melanic and non-melanic males, this would provide a mechanism by which female choice could be exercised, even though the average level of courtship activity was the same in both melanic and non-melanic males. Initially, the evolution of female mating preferences must depend on a selective advantage of the preferred males: a female with a preference will only be selected if the male she prefers gives her fitter offspring. As the mating preference evolves, it adds to the advantage of the preferred males. The male offspring of the preferential matings will have the preferred character and will also tend to carry the gene for the preference. Selection of the preferred character also selects the preference: they both evolve together with the genes in linkage disequilibrium. This is Fisher's (1930) " runaway process " of sexual selection, which O'Donald (1962, 1967) analysed in detail using computer models.

The evolution of mating preferences in the females must depend on genetic variation in female response. For example, a preference might evolve by the selection of a gene that lowers the females' threshold of response to the phenotype of the preferred male. Then if pairing takes place within a group of Arctic Skuas, and some females have lower thresholds towards the melanic phenotypes, they will soon pair with any unmated melanic male in the group. If these females find no males of their choice, they will pair later and at the same time as the remaining females: such matings will therefore take place at random among the remaining males since all the females left to mate will have the same higher average threshold towards each of the different male phenotypes. This process of mate selection corresponds to the P models. If some females prefer dark males and others prefer intermediates the mating preferences would correspond to those of model 4. A particular model of mate selection—for example, model 4P—can thus be described in terms of a specific behavioural mechanism.

Variation in female response is unlikely to be as clear-cut as this model implies. The gene for the mating preference may lower a female's threshold by a certain average amount. If the mean difference in threshold were less than about three standard deviations of the threshold distribution, the altered threshold to melanic males in some females would overlap the unaltered threshold in other females. Some preferential and random matings would therefore take place simultaneously. A combined P and S model would then be appropriate.

In the following paper in this series, O'Donald and Davis, (1977), show that model 4P has the highest likelihood of all the models of mate selection, given all the data of the breeding of the different male phenotypes up to the season of 1976. Earlier data, up to 1962, gave 4R the highest likelihood, but these data were insufficient to discriminate between the P, R and S models which all had very similar likelihoods.

5. Analysis of models of mate selection

I have described three different behavioural mechanisms that would give rise to sexual selection. An attempt must now be made to discriminate between them according to the mating behaviour of the Arctic Skua. Some models may thus be eliminated. Others may be eliminated if they give rise to significant deviations from the distributions of breeding dates and the frequencies of mating types (O'Donald, Wedd and Davis, 1974; Davis and O'Donald, 1976*b*). The results of fitting the distributions of breeding dates are described in detail in the following paper in this series (O'Donald and Davis, 1977).

The model in which territory size determines mating success has already been refuted as an explanation of the sexual selection for melanism in the Arctic Skua. It is based on the assumption that females arrive on the breeding grounds at random so that males with larger territories are more likely to encounter females. But when males have changed their mate, observations show that their new mate usually came from an adjacent territory. This is when the largest correlation between territory size and breeding time is observed. The correlation is much smaller (but not significantly different, given our rather small sample sizes) when males are breeding for the first time. Since the sexual selection is strongest when males are breeding for the first time, these facts show that territory size cannot be the principal cause of sexual selection.

Observations also indicate that the pairing of birds breeding for the first time takes place in " clubs ", or groups of young birds occupying particular areas, rather than on territories distributed throughout the Arctic Skua colony. Observations of behaviour in the clubs have not so far been carried out systematically or in detail. At present the young birds in the clubs are not colour-ringed and particular individuals cannot be followed. However, the fledglings are now being ringed with particular colour combinations of rings and will thus be identifiable when they return to the colony as immature non-breeding birds. It seems likely that pairing takes place in the clubs before the birds are ready to breed. Loose pairs can be observed between birds in a club even though they do not necessarily breed. A pair thus formed may then breed in subsequent years.

The size of the clubs and the duration of pairing affect the predictions of the models and the goodness of fit to the data. In both the P and R models, the pairing takes place in groups, females with the higher thresholds taking longer to respond to the males' courtship. The size of the group is important: it determines some of the consequences of the models. In fitting the models to the data, the breeding season was arbitrarily divided into successive intervals. The number of pairs in a particular interval was considered to be the number of females in the group who were ready to breed and who would then mate in that interval. By dividing the breeding season into smaller and smaller intervals, a point is reached at which only one female mates at a time, the females arriving to mate successively. Both the P and R models then give identical results to the S models in which preferential and random matings occur simultaneously. For example, O'Donald and Davis (1977) give estimates of the proportions of females with preferences either for dark or for intermediate males according to the P, R and S models. In these calculations, the breeding season was divided into weekly intervals. In the P models, 43 per cent of females had preferences; in the R models, 25 per cent had preferences; and in the S models, 34 per cent had preferences. However, if the size of the interval is reduced from weeks to days, the estimates of the preferences obtained from the P and R models converge on those from the S models. Eventually, when each interval contains only one female, the P and R models give the same estimates as the S models. The highest likelihood is obtained from the P models with weekly intervals. Unfortunately, the differences between the P, R and S models are not quite statistically significant. Detailed observations on the sizes of the clubs in which pairing takes place, the sequence of pairing and the length of time taken to form pairs are thus required to discriminate between these models, and hence between the behavioural mechaisms on which they depend.

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