

NOTES AND COMMENTS

SEXUAL SELECTION AND TERRITORIAL BEHAVIOUR

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It was Darwin's idea that the females of a species may exercise a mating preference for the more highly adorned males. Their adornments will thus be enhanced. An advantage may also be gained by those males who in actual combat for the females are the victors. Fighting will select the stronger and better armed of the males. Darwin believed that these two processes would account for many of the striking differences in form often to be seen between the sexes.

If sexual selection is to be effective, the successful males must leave more offspring. This they will do in a polygamous species if they can mate with more females than the unsuccessful males. Darwin thought that sexual selection would also be effective even if monogamy were the rule. The females that are the first to breed in the spring are likely to rear more offspring. They will do so because of their better nourished condition which also caused their earlier breeding. But when they return to the breeding territories these earlier females will have the first choice of the males. They will be able to unite with the more powerful and more highly endowed males. The remaining males will have to mate later with the retarded females. The better endowed males will thus pass on their better endowments to their more numerous offspring. It is now well known that in birds the number of chicks fledged does in fact decline towards the end of the breeding season, so Darwin's mechanism of sexual selection could well be effective. As I found in the Arctic Skua (O'Donald, 1962) the clutch size decreases as the breeding season advances; for clutches of given size, the number of chicks successfully fledged decreases; and the rate of development of the chicks is also slower later in the season.

Darwin did not try to explain the evolution of the female mating preferences and this essential part of the theory was supplied by Fisher (1930). In Fisher's words: "Whenever appreciable differences exist in a species, which are in fact correlated with selective advantage, there will be a tendency to select also those individuals of the opposite sex which most clearly discriminate the difference to be observed, and which most decidedly prefer the advantageous type." Suppose in a species of bird, certain types of male plumage are favoured in natural selection—perhaps a certain conspicuousness will enable the male to lure a predator away from the incubating female on the nest. If the female preferences are hereditary, then those females who exercise a preference to mate with males favoured in natural selection will themselves be selected. The male offspring of these matings will tend to have genotypes like their fathers. They will also carry the gene that determines the mating preference. Thus the selective advantage of these sons will also select the mating preference gene. Once the mating preference is established, it will itself add to the

selective pressure on the males. As Fisher suggests a "runaway process" will develop.

The original selective advantage could indeed have been due to sexual, not natural selection. At first, fighting between the males may put them at a disadvantage in natural selection: yet provided the stronger males who are prepared to fight for the females are thereby enabled to mate with more females or with those females likely to rear more offspring, then they will gain an advantage in sexual selection. Fighting for the females will take place if the overall advantage is in its favour. Fisher carries the argument one step further. Even though the stronger or better armed of the males emerge the victors; yet those weaker males who recognise the superiority of the stronger and who also avoid actual combat will themselves gain an advantage over the other equally weak males who engage in futile contests with dire or harmful results. And it will also be of advantage to the superior males to advertise their superiority, for even though they emerge victorious they must to some extent be weakened by fighting. Females who prefer the superior males will be selected in just the same way as if the preferred males were favoured in natural selection. Male weapons will thus evolve by two kinds of selection. They evolve to demonstrate superior prowess to other males, and at the same time the inferior males learn to avoid their superiors. The female preference too will exaggerate the weapons used in fighting. We can therefore explain why male weapons sometimes appear to have been developed beyond the limit at which they are useful in combat. They are in fact to advertise to both males and females alike the superiority of their possessors.

Territorial behaviour may also be important as a product of sexual selection. Lack's study of the Robin (1943) shows that territory is essentially a part of male display. Fighting seldom takes place: the owner of the territory merely sings at an intruder and this is usually enough to drive him away. Territorial behaviour therefore lessens the chance of actual combat between rival males. It also provides an area where display can be used not only to drive away other males but also to attract females. Sexual selection could have played a part in this evolution. Extremes of territorial behaviour may be another example of a character that sexual selection has promoted beyond its advantage in natural selection.

Wynne-Edwards (1962) has strongly upheld the view that male display, territory and even the whole social structure of an animal population have evolved by inter-group selection. It has indeed often been said that territorial behaviour will have advantages for a group of animals occupying a particular area. There are, however, great difficulties in any view that ascribes the evolution of a character to selection between different groups of individuals. Wynne-Edwards assumes that animal populations are split into small, more or less isolated groups. In their reproduction as a group some groups will be more efficient than others. They survive: the others die out. The more efficient groups are thus selected. This theory demands that hereditary differences should exist between the groups. How can these differences arise? On Wynne-Edwards hypothesis they cannot arise by natural selection. Can they arise by genetic drift? Now it has been shown—for example in Falconer (1960)—that only very slight migration is needed to overcome genetic drift: no more than one migrant must arrive in every second generation or genetic drift is ineffective. Very few populations can be as isolated as this. Wynne-Edwards assumes that

if a new mutation is advantageous for the group it cannot be advantageous for an individual. If this be so it is difficult to see how the new mutation can ever establish itself: both drift and selection will work for its removal. It is a very naive view of natural selection, however, to suppose that by not reproducing an individual who for example lacks a territory must always put itself at a disadvantage. Certainly if natural selection be excluded so too is sexual selection, for a mating preference can hardly have a selective advantage under group selection. Male display for example is often as important in preventing the males from fighting as it is in securing a mate. I have extended Fisher's theory of sexual selection to explain how the same display will come to serve these two functions. Wynne-Edwards, however, believes that display is entirely the product of group selection. There is of course no genetic evidence for or against these two opinions.

To show that natural selection need not always favour reproduction, I invoke Fisher's concept that natural selection acts to reduce the parental expenditure of effort devoted to the rearing of young. Fisher says: "There is something like a relic of creationist philosophy in arguing from the observation, let us say, that a cod spawns a million eggs, that therefore its offspring are subject to Natural Selection; and it has the disadvantage of excluding fecundity from the class of characteristics of which we may attempt to appreciate the aptitude. It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction." The parental resources devoted to reproduction will have an optimum value under natural selection. This optimum will represent a balance between the reproductive value of the parents and the reproductive value of their offspring. Reproduction must reduce the chances of survival of the parents; but through their offspring they will have a chance of adding their hereditary factors to those of future generations. In any one year the survival of the parents must be balanced against the survival of their offspring. A parent can either add to the next year's population through his offspring at the possible expense of his own life, or he can wait until next year to reproduce and so increase his own chances of survival. The very high death rate of young animals especially in hard years will make this choice a real one. In some years the balance of survival will fall against reproduction: other years will favour it.

Within their optimum expenditure, the parents must reproduce as efficiently as possible. Fisher used this idea to account for the equal numbers of the two sexes. Edwards (1960) has stated the idea very concisely: "The selective force arises through the advantage of reproducing as efficiently as possible—that is of making the maximum genetic contribution to future generations for a given amount of effort devoted to the bearing of young." Suppose for example that territorial behaviour increases the chances of survival of the parents; then in Fisher's terms the parental expenditure has been reduced, and as a corollary for a given amount of parental expenditure more young can be reared. Less effort too may be involved in searching for a nesting site in a less crowded place than in trying to breed in a dense colony where much effort will be spent competing

with one's neighbours. If the overall advantage favours a territory sexual selection may now operate by the Fisher process to increase the territorial instincts beyond their advantage in natural selection. It would be interesting to compare the yearly death rates of parents and offspring from territories of different sizes and the yearly death rate of unmated individuals.

Fisher's concept of making the greatest contribution to future generations for a given amount of parental expenditure on reproduction provides a possible explanation of how territorial behaviour can be favoured in natural selection. Sexual selection may exaggerate this selective effect so that territory, display and social structure all evolve together. There is no need to postulate group selection which is of doubtful validity for any evolutionary mechanism. Perhaps many of the examples of the apparent adaptation of populations rather than individuals should be examined again with the help of Fisher's theory.

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CHLORIS GAYANA WITHOUT ANTHOCYANIN COLOURATION

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Rhodes grass (*Chloris gayana* Kunth), an important ley grass in the tropics, normally has a distinct purple colouration on the spikelets, the racemes of the panicle, the nodes of the stem, the lower leaf-sheaths and on the coleoptile in the seedlings. In northern Kenya (Baringo, Sigor, Marsabit) near the northern limits of *Chloris gayana* in East Africa, the purple colour is often less evident and there are forms with yellowish panicles only slightly tinged with purple. Plants without any anthocyanin colouration occur only very occasionally. In 1958 a few non-purple plants were found at the Kitale Grassland Research Station, in a seed field of the tetraploid (Bogdan, 1961) "Mbarara" variety (Kitale Introduction No. K53166) and four such plants were transplanted to an isolated plot. In the non-anthocyanin plants the young panicles are bright yellow in colour and these plants will further be referred to as Yellow (Y) as distinct from the normal Purple (P) plants. It was thought that the non-purple plants of *Chloris gayana* were recessive and homozygous for their colour genes and could, therefore, be used for studies of breeding behaviour and