

homografts in the standard manner. The operative techniques used were satisfactory since the autografting of skin was consistently successful.

In contrast to the observations of Werder and Hardin^{1,2}, we were unable to demonstrate any beneficial effect on the survival of homografted skin after repeated grafting from either specific or random donors to either splenectomized or non-splenectomized recipients.

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¹ Werder, A. A., and Hardin, C. A., *Surgery*, **35**, 405 (1954).

² Werder, A. A., and Hardin, C. A., *Surgery*, **36**, 371 (1954).

Group Selection and Kin Selection

WYNNE-EDWARDS^{1,2} has argued persuasively for the importance of behaviour in regulating the density of animal populations, and has suggested that since such behaviour favours the survival of the group and not of the individual it must have evolved by a process of group selection. It is the purpose of this communication to consider how far this is likely to be true.

The strongest arguments for believing that conventional behaviour is the immediate cause regulating population density concern cases of territorial behaviour, particularly in birds. But it does not follow that such behaviour has evolved by group selection, because territorial behaviour capable of adjusting the population density to the available food supply could evolve by selection acting at the level of the individual rather than of the group. The appropriate degree of aggression would evolve if: (1) individuals which are too aggressive raise fewer offspring, either because they suffer physical damage or because they waste in display time and energy which should be spent in raising their young; (2) individuals which are too timid either fail to establish a territory or establish one too small to contain an adequate food supply for the young. Further, the degree of 'choosiness'—that is, the readiness to fight for a territory in one kind of area rather than put up with one in a less favourable area—will evolve by individual selection in such a way as to lead to an efficient distribution in space. This will happen because if, on one hand, individuals are too 'choosy', territories in the favoured areas will become too small in relation to the food supply, so that less choosy individuals breeding in the less favoured but more sparsely inhabited areas will leave more offspring, whereas if individuals are too little choosy, selection will act in the reverse direction.

Thus there is no need to invoke group selection to explain the evolution of individual breeding territories, or the adjustment of territory size to food supply or to variations in the habitat. But there are other characteristics of animals which are more difficult to explain by individual selection; sex is an obvious and important example, but difficulties also arise in explaining the evolution of 'altruistic' characters, such as alarm notes or injury-feigning in birds.

It is possible to distinguish two rather different processes, both of which could cause the evolution of characteristics which favour the survival, not of the individual, but of other members of the species. These processes I will call kin selection and group selection, respectively. Kin selection has been discussed by Haldane³ and by Hamilton⁴.

By kin selection I mean the evolution of characteristics which favour the survival of close relatives of the affected individual, by processes which do not require any discontinuities in population breeding structure. In this sense, the evolution of placenta and of parental care (including 'self-sacrificing' behaviour such as injury-feigning) are due to kin selection, the favoured relatives being the children of the affected individual. But kin selection can also be effective by favouring the siblings of the affected individuals (for example, sterility in social insects, inviability of cotton hybrids due to the 'corky' syndrome⁵) and presumably by favouring more distant relatives. There will be more opportunities for kin selection to be effective if relatives live together in family groups, particularly if the population is divided into partially isolated groups. But such partial isolation is not essential. In kin selection, improbable events are involved only to the extent that they are in all evolutionary change—in the origin of genetic differences by mutation.

If groups of relatives stay together, wholly or partially isolated from other members of the species, then the process of group selection can occur. If all members of a group acquire some characteristic which, although individually disadvantageous, increases the fitness of the group, then that group is more likely to split into two, and in this way bring about an increase in the proportion of individuals in the whole population with the characteristic in question. The unit on which selection is operating is the group and not the individual. The only difficulty is to explain how it comes about that all members of a group come to have the characteristic in the first place. If genetically determined, it presumably arose in a single individual. It cannot be pictured as spreading to all members of a group by natural selection, because if it could do that, it could equally well spread in a large population—either by individual selection or kin selection—and there is no need to invoke a special mechanism of group selection to explain it. Hence the only way in which such a characteristic could spread to all members of a group would be by genetic drift. (There is also the possibility that it might spread through a group by cultural transmission, but this is unlikely to be important in animals other than man.) If this were to happen at all often, then the groups must be small (or else commonly re-established by single fertilized females or single pairs), the disadvantage of the characteristic to the individual slight, and the gene flow between groups small, because every time a group possessing the socially desirable characteristic is 'infected' by a gene for anti-social behaviour, that gene is likely to spread through the group. These conditions are severe, although they may sometimes be satisfied.

The distinction between kin selection and group selection as here defined is that for kin selection the division of the population into partially isolated breeding groups is a favourable but not an essential condition, whereas it is an essential condition for group selection, which depends on the spread of a characteristic to all members of a group by genetic drift.

Wynne-Edwards² points out that birds may return after migration to the precise spot where they were raised, and argues that this would favour the operation of group selection. This is not so. What is required for group selection is that the species should be divided into a large number of local populations, within which there is free interbreeding, but between which there is little gene flow. The mere fact that many birds breed near where they were born does not bring about this situation; it would favour the operation of kin selection, but it is difficult to see how kin selection could bring about the evolution of many of the types of population-regulating behaviour which Wynne-Edwards believes he has discovered.

Wynne-Edwards also argues that the behavioural mechanisms he hypothesizes would be proof against the occurrence by mutation and subsequent spread of anti-

social behaviour patterns because of genetic homeostasis. This is a piece of special pleading: it also shows a misunderstanding of the situations in which homeostasis of this kind is to be expected. Both genetical theory and the experimental evidence suggest that if natural selection has been pushing a character in a given direction for a long time, it will be difficult for selection to produce further change in the same direction, but comparatively easy to produce a change in the reverse direction. Thus it would only be plausible to suggest that there are genetic reasons why anti-social behaviour should not increase if it were also suggested that selection had already produced an extreme degree of anti-social behaviour, and this is precisely what Wynne-Edwards denies. In fact, 'anti-social' mutations will occur, and any plausible model of group selection must explain why they do not spread.

There is one special form of group selection which is worth considering in more detail, because it can, perhaps, explain the evolution of 'self-sterilizing' behaviour; that is, behaviour which leads an individual not to breed in circumstances in which other members of the species are breeding successfully. (This is quite different from behaviour which leads individuals not to breed when other members of the species are attempting unsuccessfully to breed, or to produce fewer offspring when conditions are such that they would be unable to raise a larger number; such behaviour, although of great interest, presents no special difficulty to a selectionist.) The difficulty is that if the difference between breeders and non-breeders is genetically determined, then it is the breeders whose genotype is perpetuated.

A possible explanation is that what is inherited is the level of responsiveness to the presence of other breeding individuals. Thus suppose that there are aggressive A individuals which continue to breed or to attempt to breed at high densities, and timid a individuals, which are discouraged from breeding when the density of breeding individuals reaches a certain level, the difference between A and a being genetically determined. In a mixed group of A and a individuals, if the density is high, only A will breed, and a will be lost from the group. In a group of A individuals at high density all will attempt to breed, with the consequence that the food supply may be exhausted and the group produce few progeny. In a group consisting entirely of a individuals, at high densities some will breed and some will not, the difference between breeding and non-breeding individuals being due to age, to previous environmental history, or even to chance. Consequently an a group is less likely to outstrip its food supply, and so will leave more progeny. The difference between A and a groups at high densities is an example of the difference between a scramble (A) and a contest (a) (ref. 6).

Given such a behavioural difference, the following conditions seem necessary if a is to increase under natural selection:

- (1) Groups must for a time be reproductively isolated, because a is eliminated from mixed groups.
- (2) Groups must be started by one or a few founders, since otherwise groups consisting entirely of a individuals would never come into existence.
- (3) When a group of A individuals outstrips its food supply, it must not immediately encroach on the food supply of neighbouring a groups, for if it did so, the advantage of a groups would disappear. This is a difficult condition to meet, and appears to rule out this mechanism in cases in which the population is divided into herds, flocks, troops or colonies, each group having a joint feeding territory which borders that of neighbouring groups. The condition is most likely to be met when the food supply is discontinuous in space, each patch of food supporting its own group.

A greatly oversimplified model of this type of selection will now be given. To fix ideas, suppose that there exists a species of mouse which lives entirely in haystacks. A single haystack is colonized by a single fertilized female,

whose offspring form a colony which lives in the haystack until next year, when new haystacks are available for colonization. At this time, mice migrate, and may mate with members of other colonies before establishing a new colony. The population consists of aggressive A and timid a individuals, timidity being due to a single Mendelian recessive; a/a are timid, and A/a and A/A aggressive.

Only when a colony is started by an a/a female fertilized by an a/a male will it consist finally of a individuals; all other colonies will lose the a gene by selection, and come to consist entirely of A individuals. Thus at the time when colonies are about to break up, there are only two kinds of colony, A and a . It is assumed that an a colony contributes $1 + K$ times as many mice to the migrating population as does an A colony, and has a proportionately greater chance of having a daughter colony.

In one summer, let the frequency of a colonies be P_0 . Then, in the migrating population, the proportion of a/a individuals is:

$$\frac{P_0(1+K)}{P_0(1+K) + 1 - P_0} = \frac{P_0(1+K)}{1 + KP_0} = p \text{ say}$$

It is assumed that a proportion r of all migrating female mice mate with males from their own colony, the remaining $(1-r)$ mating at random. Hence the frequency of $a/a \times a/a$ mating as a fraction of all matings is

$$rp + (1-r)p^2 = P_1$$

where P_1 is the frequency of a colonies in the next summer.

Hence the condition for the evolutionary spread of 'timid' behaviour—that is, of the a gene—is:

$$rp + (1-r)p^2 > P_0, \text{ where } p = \frac{P_0(1+K)}{1+KP_0}$$

This reduces to

$$r(1+K) - (1 - P_0K^2) > 0$$

Thus when P_0 is large ($P_0 \approx 1$),

$$r + K > 1$$

and when P_0 is small ($P_0 \approx 0$),

$$r(1+K) > 1$$

Thus, if there is little or no interbreeding between colonies even at migration ($r \approx 1$), timid behaviour will evolve provided it is an advantage to the group; this corresponds to the case in which the population is divided into more or less permanently isolated groups, which are periodically reduced to very small numbers, and which may either become extinct or split to give rise to two groups. However, the conclusion that timid or altruistic behaviour can readily evolve if there is no interbreeding between groups means little, since it is unlikely that species are often divided into a large number of small and completely isolated groups.

If there is fairly free interbreeding between colonies at regular intervals (that is, if r is small), selection could maintain the gene for timidity once it had become the common allele in the population. For example, if there were random mating, $r = 0$, between members of different colonies at the time of migration, then selection could maintain a as the common allele if a colonies had a two-fold advantage. But, with random mating, selection could not cause a to increase if it were initially rare: if $r = 0$, the condition $r(1+K) > 1$ cannot be satisfied.

With an intermediate amount of gene flow between colonies, selection could both establish and maintain timid or altruistic behaviour, provided that colonies with altruistic behaviour have a large selective advantage, and that colonies are founded by very few individuals.

The model is too artificial to be worth pursuing further. It is concluded that if the admittedly severe conditions listed here are satisfied, then it is possible that behaviour

patterns should evolve leading individuals not to reproduce at times and in circumstances in which other members of the species are reproducing successfully. Whether this is regarded as an argument for or against the evolution of altruistic behaviour by group selection will depend on a judgment of how often the necessary conditions are likely to be satisfied.

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¹ Wynne-Edwards, V. C., *Animal Dispersion in Relation to Social Behaviour* (Oliver and Boyd, Edinburgh and London, 1962).

² Wynne-Edwards, V. C., *Nature*, **200**, 623 (1963).

³ Haldane, J. B. S., *New Biology*, **18**, 34 (1955).

⁴ Hamilton, W. D., *Amer. Nat.*, **97**, 354 (1963).

⁵ Stephens, S. G., *J. Genet.*, **50**, 9 (1950).

⁶ Nicholson, A. J., *Austral. J. Zool.*, **2**, 9 (1955).

DR. MAYNARD SMITH'S communication raises a good many more questions than I can attempt to answer here. The major obstacle to constructive discussion between us really arises from the understandable (though regrettable) differences in outlook and experience between a laboratory geneticist and a field ecologist. To me his picture of territorial systems and other aspects of conventional behaviour appears scarcely true or comprehensive enough to provide a basis for valid deduction; my own grasp of the genetical theory of natural selection, on the other hand, no doubt looks still more halting and inept to him. We ought to enlarge the area of common ground, but that is too big a task to discharge effectively here.

It is not permissible to isolate 'territory' in Dr. Smith's sense from the other overlapping forms of real property won and defended by animals, such as nest-sites of colonial birds, basking or resting places of, say, seals or crocodiles, roosting perches of starlings or domestic fowls, display arenas of manakins or bower-birds, burrows of foxes or beach crabs, and so on. Many of these have no direct connexion with food or with rearing families; but all are indissociably bound up with the status of their possessor in the social system to which he belongs, and the rights which this status confers. What we have to explain is how social systems can evolve and their conventional machinery be perfected. What appears to be inevitably required is a process of selection discriminating between one social system and another.

Social systems are collective entities, in the higher animals frequently involving an element of tradition as well as genetic transmission as they pass down from generation to generation. They entail codes of behaviour with which the individual members instinctively comply, even when compliance demands the resignation of rights to vital resources or to reproduction. The hereditary compulsion to comply, for example, in lemmings doomed to emigrate or sticklebacks inhibited from maturing by the inescapable domination of an α male, is the real keystone of social adaptation. Individuals submitting to total deprivation are eliminated altogether, most often before they have produced any offspring; yet the tendency to comply is renewed in every subsequent generation and is not bred out. One is bound to conclude that it is very securely buffered from 'ordinary' selection acting against submissive individuals and at the same time promoting their dominant sibs; and from the effects of simple Mendelian situations of the A/a type in Dr. Smith's model. I stand corrected if it is technically wrong to think of this as genetic homeostasis; the apparent result is the same. The situation I describe here is real and not, I think, controversial; it is the explanation which presents difficulties.

Most ecologists would agree that the prerequisite of group selection that calls for a subdivided population structure is commonly and indeed normally found in animals. Dr. Smith says that the *Ortstreue* or return of

migrant birds to their native locality would not bring it about; perhaps it is easier to see than in the case of the salmon or trout spawning in its natal tributary stream, where it more obviously becomes a member of a partially isolated breeding group.

The model of the mice in the haystacks is not, perhaps, a sufficiently close approximation to any natural situation to help us far towards a solution. A realistic counterpart might be, for example, the woodlice (*Porcellio scaber*) that fed on the green alga *Protococcus* living on tree-trunks, studied by Brereton¹; marked woodlice confined their feeding to their own particular tree, and the population appeared to be subdivided thus into breeding units. Had any of the latter increased too freely they could have exterminated their stock of this particular food plant, which does not regenerate easily. Supposing in Dr. Smith's model that all the A colonies grow so fast that they finish the food and die of starvation before "migration time" arrives; then $K = \infty$, $p = 1$, $r = 1$, and $P_1 = 1$, and group selection wins the trick!

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¹ Brereton, J. Le G., *Oikos*, **8**, 85 (1957).

Survival of Young Swifts in Relation to Brood-size

In a recent article in *Nature*, Wynne-Edwards¹ said "the assumption, still rather widely made, [is] that under natural selection there can be no alternative to promoting the fecundity of the individual, providing this results in his leaving a larger contribution of progeny to posterity. This assumption is the chief obstacle to accepting the principle of intergroup selection".

Wynne-Edwards implies that this assumption is wrong, but omits to note that there are data which show that at least some species are producing as many surviving young as possible, for example, the starling, *Sturnus vulgaris*², the great tit, *Parus major*³, and the laysan albatross, *Diomedea immutabilis*⁴. The swift (*Apus apus*) is a convenient species for a study of this kind since, like the albatross but unlike the passerine species studied, considerable mortality, due to starvation, occurs in the nest.

In England the swift normally lays a clutch of two or three eggs, clutches of four being very rare indeed (less than 0.25 per cent)^{5,6}, and it is interesting to consider what would happen if a larger clutch were laid. One cannot hope to observe a natural change (presumably a genetical mutation) which results in enough swifts laying clutches of four eggs instead of three to provide significant samples. However, by transferring young at hatching it is possible to compare the survival of young from broods of four with that from broods of two and three.

Swifts feed exclusively on airborne arthropods⁷, the availability of which is greatly affected by the weather. In cold, wet summers the arthropods are less active and therefore less available to the swifts than in fine weather. At Oxford, Lack⁵ showed that in fine summers the average number of young produced per brood was highest from broods of three whereas in cold, wet summers it was highest from broods of two.

In the summers of 1958-61 inclusive I increased some broods of swift to four young by adding a newly hatched chick at the time that a fourth egg would have been expected to hatch. Subsequent survival is summarized in Table 1. In the summers of 1958, 1960, and 1961, the weather, and therefore the feeding conditions for swifts, were fairly good, and in 1959 they were exceptionally so. (Following the method used by Lack⁵, the mean maximum temperatures during the nestling period were 68, 70, 72 and 70° F for the four years, respectively.)