

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

<sup>2</sup> Wynne-Edwards, V. C., *Nature*, **200**, 623 (1963).

<sup>3</sup> Haldane, J. B. S., *New Biology*, **18**, 34 (1955).

<sup>4</sup> Hamilton, W. D., *Amer. Nat.*, **97**, 354 (1963).

<sup>5</sup> Stephens, S. G., *J. Genet.*, **50**, 9 (1950).

<sup>6</sup> 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  $\alpha$  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 then 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 Brereton<sup>1</sup>; 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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<sup>1</sup> Brereton, J. Le G., *Oikos*, **8**, 85 (1957).

### Survival of Young Swifts in Relation to Brood-size

In a recent article in *Nature*, Wynne-Edwards<sup>1</sup> 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*<sup>2</sup>, the great tit, *Parus major*<sup>3</sup>, and the laysan albatross, *Diomedea immutabilis*<sup>4</sup>. 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)<sup>5,6</sup>, 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 arthropods<sup>7</sup>, 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, Lack<sup>5</sup> 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 Lack<sup>5</sup>, the mean maximum temperatures during the nestling period were 68, 70, 72 and 70° F for the four years, respectively.)