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Author(s): W. D. Hamilton

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THE EVOLUTION OF ALTRUISTIC BEHAVIOR

It is generally accepted that the behavior characteristic of a species is just as much the product of evolution as the morphology. Yet the kinds of behavior which can be adequately explained by the classical mathematical theory of natural selection are limited. In particular this theory cannot account for any case where an animal behaves in such a way as to promote the advantages of other members of the species not its direct descendants at the expense of its own. The explanation usually given for such cases and for all others where selfish behavior seems moderated by concern for the interests of a group is that they are evolved by natural selection favoring the most stable and co-operative groups. But in view of the inevitable slowness of any evolution based on group selection compared to the simultaneous trends that can occur by selection of the classical kind, based on individual advantage, this explanation must be treated with reserve so long as it remains unsupported by mathematical models. Fisher in the second edition of "The Genetical Theory of Natural Selection" (1958) rejects almost all explanations based on 'the benefit of the species' (e.g., p. 49). Sewall Wright (1948) in a summary of population genetics shows explicitly that a general advantage conferred on a group cannot alter the course of intragroup selection. This point is very adverse to the following model of Haldane (1932, p. 208) which seemed to offer a possibility for the evolution of altruism. Haldane supposed an increment to group fitness (and therefore to group rate of increase) proportional to its content of altruistic members and showed that there could be an initial numerical increase of a gene for altruism provided the starting gene frequency was high enough and the individual disadvantage low enough compared to the group advantage conferred. He concluded that genetical altruism could show some advance in populations split into 'tribes' small enough for a single mutant to approximate the critical frequency. He did not, however, sufficiently emphasize that ultimately the gene number must begin to do what the gene frequency tends to do, *ex hypothesi*, from the very first; namely, to decrease to zero. The only escape from this conclusion (as Haldane hints) would be some kind of periodic reassortment of the tribes such that by chance or otherwise the altruists became re-concentrated in some of them.

There is, however, an extension of the classical theory, generalizing that which serves to cover parental care and still having the generation as the time-unit of progress, which does allow to a limited degree the evolution of kinds of altruism which are not connected with parental care.

As a simple but admittedly crude model we may imagine a pair of genes g and G such that G tends to cause some kind of altruistic behavior while g is null. Despite the principle of 'survival of the fittest' the ultimate criterion which determines whether G will spread is not whether the behavior is to the benefit of the behaver but whether it is to the benefit of the gene G ; and this will be the case if the average net result of the behavior is to add to the gene-pool a handful of genes containing G in higher concentration

than does the gene-pool itself. With altruism this will happen only if the affected individual is a relative of the altruist, therefore having an increased chance of carrying the gene, and if the advantage conferred is large enough compared to the personal disadvantage to offset the regression, or 'dilution,' of the altruist's genotype in the relative in question. The appropriate regression coefficient must be very near to Sewall Wright's Coefficient of Relationship r provided selection is slow. If the gain to a relative of degree r is k -times the loss to the altruist, the criterion for positive selection of the causative gene is

$$k > \frac{1}{r}.$$

Thus a gene causing altruistic behavior towards brothers and sisters will be selected only if the behavior and the circumstances are generally such that the gain is more than twice the loss; for half-brothers it must be more than four times the loss; and so on. To put the matter more vividly, an animal acting on this principle would sacrifice its life if it could thereby save more than two brothers, but not for less. Some similar illustrations were given by Haldane (1955).

It follows that altruistic behavior which benefits neighbors irrespective of relationship (such as the warning cries of birds) will only arise when (a) the risk or disadvantage involved is very slight, and (b) the average neighbor is not too distantly related.

An altruistic action which adds to the genotype-reproduction (inclusive of the reproduction of identical genes procured in the relative) by one per cent is not so strongly selected as a one per cent advantage in personal reproduction would be; for it involves also an addition of unrelated genes which are in the ratio of the existing gene-pool—an addition which must be larger the more distant the relationship.

A multi-factorial model of inheritance, which is doubtless more realistic, does not invalidate the above criterion, and provided fitness is reckoned in terms of 'inclusive' genotype-reproduction, and the dilution due to unrelated genes is allowed for, the classical treatment of dominance and epistasis can be followed closely.

Fisher in 1930 (1958, p. 177 et seq.) offered an explanation of the evolution of aposematic coloring based on the advantage to siblings of the self-sacrifice, by its conspicuousness, of a distasteful larva, and his discussion contains what is probably the earliest precise statement concerning a particular case of the principle presented above: "The selective potency of the avoidance of brothers will of course be only half as great as if the individual itself were protected; against this is to be set the fact that it applies to the whole of a possibly numerous brood." It would appear that he did not credit the possibility that selection could operate through the advantage conferred on more distant relatives, even though these must in fact tend to be still more numerous in rough inverse proportion to the coefficient of relationship.

This discussion by Fisher is one of the few exceptions to his general insistence on individual advantage as the basis of natural selection; the other notable exception from the present point of view is his discussion of putative forces of selection in primitive human societies (p. 261 et seq.).

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W. D. HAMILTON

DEPARTMENT OF SOCIOLOGY
LONDON SCHOOL OF ECONOMICS
LONDON, WC2
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