



Group Selection

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COMMENTARY

GROUP SELECTION

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A consideration of *Group Selection in Predator-Prey Communities*, by M. E. Gilpin (Princeton University Press, 1975), and other recent discussions of group selection.

INTRODUCTION

THE PURPOSE of this short review is to look at some recent discussions of group selection, in particular those by E. O. Wilson (1975), D. S. Wilson (1975) and M. E. Gilpin (1975). Earlier work will be referred to only briefly; the need for a review arises because the three references given either propose a blurring of the distinction between "group" and "kin" selection, or suggest an importance for group selection greater than it has usually been given, or both.

The first point to establish is that the argument is quantitative, not qualitative. Group selection will have evolutionary consequences; the only question is how important these consequences have been. If there are genes which, although decreasing individual fitness, make it less likely that a group (deme or species) will go extinct, then group extinction will influence evolution. It does not follow that the influence is important enough to play the role suggested for it by some biologists.

The present phase of the debate about group selection was opened by the publication of Wynne-Edwards' "Animal Dispersion" (1962), which applied to animals a concept first proposed by Carr-Saunders (1922) to explain human population dynamics; it ascribed to group selection a major role in the evolution of population regulation. Although his thesis has had its adherents, the orthodox response from ecologists has been to argue that the

patterns of behavior he described can be explained by individual selection, and from population geneticists that the mechanism he proposes is insufficient to account for the results. It is in the nature of science that once a position becomes orthodox it should be subjected to criticism; hence the papers by D. S. Wilson (1975), Gilpin (1975), Levin and Kilmer (1974), Gadgil (1975), and others. It does not follow that, because a position is orthodox, it is wrong; hence this review.

Is the argument important? In a recent review of E. O. Wilson's "Sociobiology," C. H. Waddington referred to group selection as "a fashionable topic for a rather foolish controversy." Doubtless some foolish things have been said, but there is an important issue at stake. If group selection has played the role suggested by Wynne-Edwards, no one can doubt its importance. But why should it be important to argue that it has not? The reason for the vehemence with which Williams (1966, 1975), Ghiselin (1974), Lack (1966) and other opponents of group selection have argued their case is, I think, their conviction that group selection assumptions, often tacit or unconscious, have been responsible for the failure to tackle important problems. So long as we fail to distinguish group and individual selection, or assume that an explanation in terms of advantage to the species is adequate to account for the evolution of some behavior pattern or genetic process, without asking what is its effect on individual fitness, we shall make little progress.

The extent of unconscious group selection-

ism, particularly among ecologists, has recently been documented by Ghiselin (1974). Similar views are still widespread among ethologists. It is, however, in the study of the evolution of genetic mechanisms that group selection assumptions are most pervasive. Fisher (1930) argued that sexual reproduction owed its existence to the fact that sexually reproducing populations can evolve more rapidly than asexual ones. Darlington (1939) attempted to explain a wide range of adaptations in chromosome structure and recombination frequency in terms of inter-population selection. Since that time, the interpretation of genetic mechanisms in terms of species advantage has become almost commonplace.

Of course, group advantage cannot be ruled out a priori as an explanation of the evolution of ecological adaptations, of behavior or of genetic mechanisms. But the quantitative difficulties must be faced. It is plausible, for example, to suppose that, whatever its origin, sexual reproduction is maintained in higher organisms because populations which abandon sex go extinct in competition with more rapidly evolving sexual species. This plausibility depends on the assumption that the origin of new ameiotically parthenogenetic strains is a sufficiently rare event for each such origin to be balanced by the extinction of such a strain. It is less plausible to suppose that the chiasma frequency or recombination frequency within a species is determined by group selection, because there is widespread within-species genetic variation of recombination rate, and we would therefore expect individual selection acting on this variation to outweigh any long-term effects of interspecies selection.

It is not the purpose of this review to discuss the evolution of sex or recombination. The problem has been mentioned because it illustrates particularly clearly the quantitative difficulties faced by group selection explanations. In view of these difficulties, an explanation in terms of group advantage should always be explicit, and always calls for some justification in terms of the frequency of group extinction. Wynne-Edwards' great merit is that he made the assumption explicit, and in so doing forced population geneticists to make the argument quantitative.

THE DISTINCTION BETWEEN GROUP AND KIN SELECTION

The frequency of a gene in a population will be influenced not only by the effects that gene has on the survival and fertility of individuals carrying it, but also by its effects on the survival and fertility of relatives of that individual. The second kind of effect has been called "kin selection" (Maynard Smith, 1964). The effect is obvious when the "relatives" are the children or other direct descendants of the individual; it has always been appreciated that genes improving parental care will be selected. Fisher (1930) and Haldane (1932) saw clearly that the effect would work for other relatives (e.g., sibs or cousins). In the vaguer forms of "inter-family selection" the idea goes back to Darwin's *Origin of Species*.

Wright (1945) discussed the evolution of altruistic traits in terms of "interpopulation selection." Despite his use of this phrase, his model, which is sketched rather than fully worked out, would fall under the heading of kin selection rather than group selection if the distinction suggested below is accepted.

Attempts to apply the idea of kin selection in detail to the evolution, first of social insects and later of other animal societies, originated with Hamilton (1963, 1964), and are the central theme of E. O. Wilson (1975).

With the almost simultaneous publication of Hamilton's papers and Wynne-Edwards' book, it seemed desirable to draw a clear distinction between the two processes of kin and group selection, and to coin a term for the former (Maynard Smith, 1964). It is always difficult to draw unambiguous distinctions in biology, but it is often valuable to try. I still think that the attempt was on the right lines, although in retrospect I can see that there is one essential feature of group selection, namely group extinction, which I failed to emphasize, although it was present in my mathematical model. The basic distinction made concerned the population structure required for the two processes. For kin selection (as described by the first sentence in this section) it is necessary that relatives live close to one another, but it is not necessary (although it may be favorable) that the population be divided into reproductively isolated groups. All that is essential for kin

selection is that relatives live close to one another, so that an animal's behavior can influence the survival or fecundity of its relatives.

For group selection, the division into groups which are partially isolated from one another is an essential feature. If group selection is to be responsible for the establishment of an "altruistic" gene, the groups must be small, or must from time to time be re-established by a few founders. This is because in a large group there is no way in which a new "altruistic" gene can be established. If a new mutant is to be established in a large group, then it must increase the fitness of individuals carrying it, or more precisely, it must increase their "inclusive fitness" relative to other members of the group (Hamilton, 1964); if this is so, group selection is not needed to explain its spread. Small group size is not needed for the maintenance of an altruistic gene, only for its establishment. The involvement of genetic drift as an essential feature of group selection has been queried by D. S. Wilson (1975); I will return to this point later.

What I should have said in my 1964 paper, but did not, is that the extinction of some groups and the "reproduction" of others are essential features of evolution by group selection. If groups are the units of selection, then they must have the properties of variation, multiplication, and heredity required if natural selection is to operate on them. In a finite universe, multiplication implies death. Group selection could operate for a short time on differences in group reproduction, without group extinction, but in the long run evolution by group selection requires group extinction just as evolution by individual selection requires individual death.

The relevance of group reproduction and extinction can best be illustrated by a partly imaginary example. Anubis baboons live in troops; females remain in their natal troop whereas males must move to another troop before breeding (Packer, 1975). Suppose that a gene were to arise which caused females to help other females in their troop to raise their offspring (in fact, females do help one another to defend their young against males). This gene would increase in frequency in the whole population—more males would be produced by a troop whose females carried the gene, and

these males would transmit the gene to other troops. Despite the existence of troops, I would regard this as an example of kin selection. The gene would not increase in frequency unless the females in a troop were related to one another. But the increase does not depend on small group size and hence on genetic drift, nor does it depend on group reproduction or extinction; indeed, it would work in much the same way if there were no groups, provided that females bred close to where they were born, and that males dispersed before breeding.

There will doubtless be cases in which the distinction is difficult to draw. E. O. Wilson (1975) has argued that "pure kin and pure interdemic selection are the two poles at the end of a gradient of selection on ever enlarging nested sets of related individuals." In similar vein, D. S. Wilson (1975) writes "the traditional concepts of group and individual selection are seen as two extremes of a continuum." The disagreement between us, if there is one, is one of semantics and the strategy of research rather than of fact. In the history of ideas as in taxonomy, there are lumpers and splitters; I am a splitter. I think we would do best to draw as clear a distinction as we can between different processes. I welcome E. O. Wilson's distinction between inter-demic and inter-species selection, although both are forms of group selection.

Why do I think it desirable to sharpen rather than to blur the distinction between different modes of selection? Ultimately, the importance or otherwise of these different modes can only be decided by comparing different species, and asking whether particular traits, such as altruistic, prudent, or selfish behavior, are associated with particular population structures. For this to be a meaningful enterprise, we must be clear about what are the relevant features of population structure. In particular, we must be clear whether our theory asserts that the evolution of a trait requires the existence of groups, or merely that relatives should be neighbors.

To sum up, "group" selection should be confined to processes that require the existence of partially isolated groups which can reproduce and which go extinct; the origin of new altruistic traits requires that the groups be small or be founded by a few individuals. Kin selection can

operate whenever relatives live close to one another, and hence can influence one another's chances of survival and reproduction; they may or may not live in groups.

MODELS OF GROUP SELECTION

Maynard Smith (1964) proposed a model, the "Haystack" model, whereby an "altruistic" gene, which is eliminated by its "selfish" allele from mixed groups, can increase in frequency by group selection. In this model all groups necessarily became extinct since they depend on a transitory resource (a "haystack"), but groups containing only the altruistic gene produce more potential founders of new groups. In most other models of group selection, extinction has been made stochastic rather than necessary, with the probability of extinction being lower in groups with a higher frequency of the altruistic allele. Thus, in my model, groups differed in "fecundity," whereas in most subsequent models they differ in "viability."

More general models for the spread of altruistic alleles brought about by differential group extinction were proposed by Levins (1970) and by Boorman and Levitt (1973). Although different in detail, these models have in common that they confirm the logical possibility of group selection, but show that the population structure in time and space required for its operation is of a kind which may be rather infrequent in practice. Levin and Kilmer (1974) reach similar conclusions on the basis of a computer-simulated model. Genetically effective deme sizes of less than 25 and usually closer to 10 were required, and the rate of gene flow by migration could not be greater than 5 per cent per generation.

Gilpin (1975) presents a very thoroughly worked out model. His proposed mechanism is clearly a case of group selection as defined above. It is of particular interest because the altruistic trait he considers, "prudence" on the part of predators leading them not to over-exploit their food supply, is precisely the one for which Wynne-Edwards proposed group selection. The new features which Gilpin has introduced into the argument relate to the dynamics of predator-prey systems. For a wide class of models describing the interaction between a predator and prey (the model of Rosenzweig and MacArthur, 1963, is a familiar

example), a small change in the properties of the predator can cause a large change in system behavior. Suppose we start from a state of stable coexistence of predator and prey, and suppose individual selection to be acting to improve the hunting ability of the predators. The equilibrium will change gradually, with the predator numbers increasing and the prey decreasing, until a critical point is reached. If hunting ability continues to increase beyond this point, the equilibrium becomes unstable and the system passes into a stable oscillation (a limit cycle). With further improvement in hunting ability, the amplitude of the oscillation rises until, with finite populations, chance extinction of one or both species would ensue.

Gilpin imagines an environment composed of patches. A predator population may contain only genotypes *aa*, in which case stable coexistence is possible, or only *AA*, which leads to rapid extinction, or some mixture of *aa*, *Aa* and *AA*. A mixed population evolves by individual selection to the fixation of allele *A*, and hence to extinction. In his model, Gilpin allows for migration between patches, and genetic drift within them. He shows that for a reasonably wide range of parameter values the altruistic allele *a* can maintain itself against *A*.

The problem remains whether the range of parameter values includes cases likely to correspond to natural predator-prey systems. The very complexity of Gilpin's model makes this difficult to decide. Fortunately, however, I believe it possible to replace Gilpin's model of group selection (and many other models) by a much simpler model, and to identify a single parameter which will determine the fate of an altruistic gene. In Gilpin's model, there are at any moment three kinds of patch: "empty" patches, *E*, containing no predators (although they may contain prey); "altruistic" patches, *A*, containing only *aa* predators; and "selfish" patches, *S*, containing at least some *AA* or *Aa* predators. The types of patch, and the possible transitions between them, are shown in Fig. 1. The transition from *E* to *S* is shown by a broken arrow because, although it is permitted in Gilpin's model, it would not be in some other models of group selection.

The model is formally similar to one analyzed by Maynard Smith (1974), but with a different biological interpretation. In that model, *E* represented empty patches; *A*, patches with prey

individuals only; and S, patches containing both predator and prey and destined to become empty. The model is also formally similar to an unpublished model by Ivar Heuch of the University of Bergen for the evolution of the sex ratio in the butterfly *Acraea encedon*. In this species there is a "driving" Y^* chromosome, such that XY^* females have only daughters. In a panmictic population this should lead to species extinction. Heuch suggests that the species survives because of its patchy distribution. Again, E represents empty patches; A represents patches with only normal XY females; S represents "infected" patches containing at least one XY^* female and destined for extinction. In effect, Heuch's model is one of balance between gametic selection for Y^* and group selection for Y.

In such models, it is easy to see that the fate of the system depends on the single parameter M , which is the expected number of successful "selfish" emigrants from an S patch during the lifetime of the patch, from the moment it becomes "infected" to the time it becomes extinct. By a "selfish" emigrant is meant an AA or Aa predator in Gilpin's model, a predator in my model, or an XY^* female in Heuch's model. By "successful" is meant that the migrant established itself and leaves descendants in a new patch (either E or A). If $M > 1$ the frequency of S patches will increase. The continued existence of the system requires $M < 1$.

In Gilpin's model, this means that during the history of a patch, from the moment when it is "infected" by an Aa or AA immigrant to the time of its extinction, there must on the average be less than one successful Aa or AA migrant to another patch. It is thus fairly easy to understand the features of his model which make for the maintenance of prudent aa genotypes. They are small population size per patch, little migration, and rapid extinction of a patch once infected. Rapid extinction arises from the nature of the predator-prey dynamics (a plausible assumption which is Gilpin's main innovation), and from the assumption that a single gene substitution in a small population is sufficient to tip the balance from stability to extinction.

It is hard to say how often the condition $M < 1$ will hold in nature. But it may be easier to decide whether group selection is a plausible

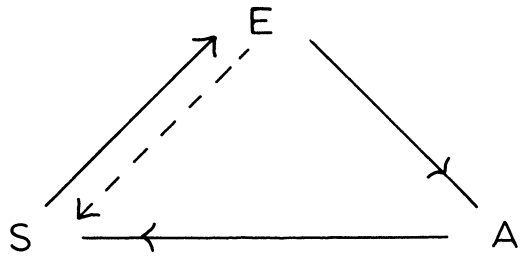


FIG. 1. A MODEL OF GROUP SELECTION
For explanation see text.

mechanism in particular cases by concentrating on this inequality than by considering all the details and parameter values of the full model.

Finally, before leaving this topic, it is helpful to note the analogy between the equilibrium condition, $M = 1$, and the well-known principle of individual selection, that the mutational load equals the mutation rate. The latter principle states that each individually harmful mutation must be balanced by a death; the former that each socially harmful infection must be balanced by an extinction.

A quite different approach to the problem of group selection is taken by D. S. Wilson (1975). He considers a population which, although breeding at random, is divided for some part of the life cycle into "trait groups," within which altruistic or selfish interactions can take place. For a pair of alleles A and a, such that a determines an altruistic behavior which decreases the individual's chance of survival but increases the survival chances of all other members of the group, he shows that a can increase in frequency, but only if the between-trait-group genetic variance is greater than random—i.e., than would be expected if the members of trait groups were a random sample of the whole population.

This is an interesting result, but seems to me to refer to kin selection and not to group selection. Indeed, there is no reason other than mathematical convenience why he should consider trait "groups." His argument would work equally well if there were no discontinuities in spatial distribution provided that there was a genetic similarity between neighbors. The obvious reason why the members of a trait group might resemble one another genetically is that they are relatives. Wilson's result is then fully in accord with Hamilton's (1964) assertion that

an altruistic gene will increase in frequency only if $k > 1/r$, where r is the coefficient of relationship between donor and recipient, and k the ratio of the gain of fitness of the recipient to the loss of fitness of the donor. Clearly, if $r = 0$ altruism will not increase in frequency.

Wilson argues from his model that genetic drift is not needed for group selection; since I do not think he is discussing group selection, I do not find his argument convincing. In fact, it is not clear why Wilson does not regard his model as one of kin selection. For example, he writes "consider a situation in which larval insects are deposited into the trait-groups by adult females. The larvae upon hatching intermix within the trait-group, and so do not fall under the traditional concept of kin selection." This is precisely the type of situation I intended to fall under the term kin selection. If, for example, animals behave with an equal degree of altruism to all their "neighbors", or to all fellow members of their "trait-group," and if *on average* animals are related to their neighbors, then I would regard this as an example of kin selection. It is not a necessary feature of kin selection that an animal should distinguish different degrees of relationship among its neighbors, and behave with greater altruism to the more closely related.

Apart from relatedness, there are other possible reasons why members of a trait-group might resemble one another genetically. If individuals of like genotype tend to associate together, either because they are attracted to one another, or because they are attracted by common features of the environment, or because they are the survivors of a common selective force, then altruism can be selected for. Before invoking this mechanism, however, it is important to remember that if an altruistic allele a is to replace a selfish allele A , then the members of a trait-group must resemble one another *at that locus*. If they are not related in the normal sense, this would require that the altruistic locus have pleiotropic effects determining association. Thus, these other reasons for genetic

similarity between neighbors seem likely to be unimportant compared with identity by descent.

CONCLUSIONS

It is useful to distinguish as sharply as possible the processes of "kin" and "group" selection. The terms group selection should be confined to cases in which the group (deme or species) is the unit of selection. This requires that groups be able to "reproduce," by splitting or by sending out propagules, and that groups should go extinct. The origin of an altruistic trait (but not its maintenance) requires that the groups be small, or that new groups be established by one or a few founders. Kin selection requires only that relatives should live close to one another. The division of the population into groups, either permanently or for part of the life cycle, may favor the operation of kin selection but is not a necessary feature.

Group selection can maintain "altruistic" alleles—i.e., alleles which reduce individual fitness but increase the fitness of groups carrying them. The conditions under which this can happen are stringent, so that the main debate concerns whether the process has had evolutionarily important consequences. The main function of models is to indicate the circumstances in which group selection can be important. For one large class of models, it can easily be seen that the condition for the maintenance of an altruistic allele by group selection is $M < 1$, where M is the expected number of successful migrants carrying the selfish allele produced by a group during the whole period from the moment when it was first "infected" by a selfish immigrant to the times of its extinction.

It follows that the features favoring group selection are small group size, low migration rates, and rapid extinction of groups infected with the selfish allele. The ultimate test of the group selection hypothesis will be whether populations having these characteristics tend to show "self-sacrificing" or "prudent" behavior more commonly than those which do not.

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