A THEORY OF GROUP SELECTION
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ABSTRACT

A THEORY OF GROUP SELECTION

by

David Sloan Wilson

In organisms possessing a dispersal phase the processes of mating, competition, feeding and predation are often carried out in spatial areas (trait-groups) smaller than the boundaries of the deme. A simple model shows that this can lead to the selection of 'altruistic' traits that favor the fitness of the group over the individual. The extent of group selection that occurs depends mainly on the variation in the composition of genotypes between trait-groups. The traditional concepts of group and individual selection are seen as two extremes of a continuum, with systems in nature operating over the interval in between.

A THEORY OF GROUP SELECTION

By

David Sloan Wilson

A DISSERTATION

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TABLE OF CONTENTS

Page

LIST OF FIGURES

Figure Page

INTRODUCTION

The theory of group selection became controversial in 1962 when V. C. Wynne-Edwards postulated that animals hold their density below carrying capacity to avoid overexploiting their resources. Unfortunately Wynne-Edwards' ideas on how such a 'management' policy could evolve were vague and unconvincing.

Since then one of the greatest impediments to the development of the theory has ironically, been its enormous appeal. Against a Darwinian landscape of competition and selfishness, it proposes cooperation and altruism. People want to believe it, and evolutionary biologists, instead of exploring it as an exciting possibility, have until recently felt obligated to hold back a flood of uncritical acceptance with ominous reminders about parsimony.

During the last few years, however, a flush of recent models indicate that group selection is being approached in a more objective spirit (e.g., Levins 1970, Boorman and Levitt 1973, Levin and Kilmer 1974, Gilpin 1975). Most are refinements of Wynne-Edwards' initial conception of _interdemic_ selection--a cluster of small groups, completely isolated except for a trickle of dispersers. Within each group natural selection promotes increased resource utilization, even to the point of overexploitation. Groups that overexploit go extinct, however, so given a variation in the composition of genotypes between groups (created by genetic drift and founder effects) differential extinctions can create a form of 'group' selection promoting resource management. These models conclude that although group selection can be a significant force in a mathematical sense, the conditions presupposed are rarely met in nature.

Even though these models are weak, this does not mean that group selection is a weak force in nature. Traditional evolutionary theory still labors under an unreasonable assumption of spatial homogeneity of genotypes. Interdemic variation is one way to relax the assumption, but it is not the only way.

This thesis presents a simple model of group selection based on small scale, intrademic spatial variation of genotypes. The concept of intrademic spatial variation at first sounds contradictory, for a deme is by definition a spatially homogenous mating population. However, the concept is realistic due to a ubiquitous feature of organisms: Almost all plants and animals concentrate their movements in a brief dispersal stage, and it is this stage that sets the size of the deme. It follows that all traits manifested during the non-dispersal stages must occur within populations that are smaller than the deme. In short, as far as the manifestation of traits are concerned, the deme is not only a population of individuals, but also a population of groups.

When this concept is applied to traditional models, it can be shown that both individual and group selection represent absurd extremes of a continuum, with populations in nature operating over the interval in between.

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A Theory of Group Selection

(altruism/natural selection/structured demes/spatial heterogeneity)

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ABSTRACT In organisms possessing a dispersal phase the processes of mating, competition, feeding, and predation are often carried out within "trait-groups," defined as populations enclosed in areas smaller than the boundaries of the deme. A simple model shows that this can lead to the selection of "altruistic" traits that favor the fitness of the group over that of the individual. The extent of group selection that occurs depends mainly on the variation in the composition of genotypes between trait-groups. The traditional concepts of group and individual selection are seen as two extremes of a continuum, with systems in nature operating over the interval in between.

Most theories of group selection (1–6) postulate many groups fixed in space, with exchange by dispersers between groups. Within groups individual selection operates; an "altruistic" trait can thus only become fixed by genetic drift. This requires the groups to be small, and dispersal between groups must be slight to prevent the reintroduction of "selfish" individuals. The "altruistic" groups could then serve as a stock for the recolonization of selfish groups that go extinct. See ref. 7 for a review.

The recent models of Levins (4), Boorman and Levitt (5), and Levin and Kilmer (6) make it plausible that this process can occur—the main question is to what extent the conditions for its operation (small group size, high isolation, high extinction rates) are met in nature. The current consensus is that the proper conditions are infrequent or at least limited to special circumstances such as the early stage of colonization of many populations (7).

This paper presents a theory of group selection based on a different concept of groups, perhaps more generally met in nature.

Most organisms have a dispersal stage—the seeds and pollen of plants, the post-teneral migratory phase of adult insects (8), the larvae of benthic marine life, the adolescents of many vertebrates. This means that individuals are spatially restricted during most of their life cycle, with the exception of their dispersal phase, when what was previously a boundary is easily transcended. As an example, a caterpillar is restricted to one or a few plants, but as a butterfly it spans whole fields.

Evolution's most easily conceived population unit is the deme, and it is determined by the movement occurring during the dispersal phase. Yet most ecological interactions, in terms of competition, mating, feeding and predation are carried out during the nondispersal stages in the smaller subdivisions, which I term "trait-groups." In some cases the trait-groups are discrete and easily recognized, such as for vessel-inhabiting mosquitoes and dung insects. In other cases they are continuous and each individual forms the center of its own trait-group, interacting only with its immediate neighbors, which comprise a small proportion of the deme. Two examples are plants and territorial animals. The following model treats only the discrete case, but the results can be generalized.

In order to determine if a heritable trait manifested within the trait-group will be favored in selection, the effect of that trait on relative fitnesses *within the trait-group* must be modelled, and the relative fitnesses for the deme obtained by taking the weighted average over all the trait-groups in the deme. Traditional models of selection neglect this; i.e., they assume that the trait-group equals the deme.

THE MODEL

Consider a single, haploid, randomly intermixing trait-group of organisms, composed of two types of individuals, A and B. These differ by only a single heritable trait, such as feeding rate, aggressiveness, or behavior under the threat of predation. Because the two types are identical in every other respect, they will have the same "baseline" fitness, and differences can be attributed solely to the effect of the trait. Haploidy and baseline fitness are of course artificial for most populations. They are used to simplify the argument, and the fundamental conclusions are not dependent upon them. Space does not permit a fuller treatment, which will be presented elsewhere.

By manifesting its trait, every A-individual changes its own fitness and often the fitness of the other animals in the trait-group by a certain increment or decrement. Call the individual manifesting the trait the donor, and all those affected by it (both A and B types) the recipients. These terms are commonly used for altruistic social behaviors, but here they are applied to all traits. For instance, an animal with a higher feeding rate deprives its neighbors of food that otherwise would be available to them. A positive fitness change is thus bestowed upon the donor and a negative fitness change to the recipients, even though the animals never interact behaviorally with each other.

Graphically, any trait can be portrayed as in Fig. 1. Each point on the graph represents a trait with its fitness change to the donor (f_d) and to each recipient (f_r). In the example just given the trait would lie somewhere in the fourth quadrant (f_d positive, f_r negative). As another example, a warning cry might decrease the fitness of the caller (f_d negative) and increase the fitness of those that hear the cry (f_r positive),

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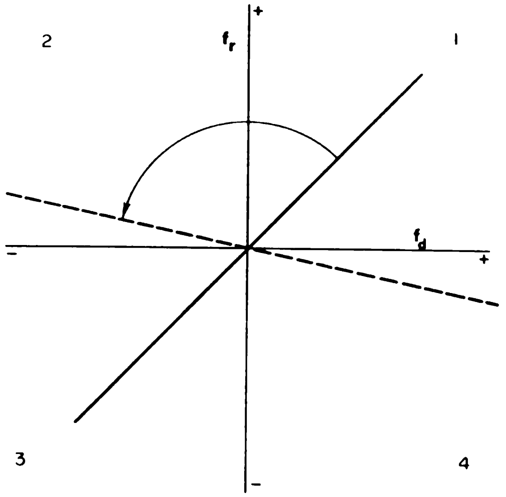

FIG. 1. The entire set of traits giving fitness changes to the donor (f_d) and to each recipient (f_r). Any point to the right of the diagonal solid line is selected for; in the position shown the solid line represents the traditional concept of individual selection ($f_d > f_r$). Any point to the right of the broken line increases the fitness of the group ($f_d > -(N - 1)f_r$). As the variation in the composition of trait-groups increases, its effect on the selection of traits is to rotate the solid line until it is coincidental with the broken line (arrow).

placing the trait somewhere in the second quadrant. In this model it is assumed that f_r is the same for both A and B types. While this will often be false in nature, it serves as a foundation for more realistic elaborations.

If N is the total trait-group size and a,b the proportions of the A and B types, respectively, the average per capita fitness changes resulting from the trait can easily be calculated.

per capita fitness change to the A-type $= f_d + N(a - 1/N)f_r$
per capita fitness change to the B-type $= Naf_r$

Traditional selection models assume that the trait-group equals the deme. In this case the model is sufficient as stands and the A-individuals are selected for only if they have a higher per capita fitness change than the B-individuals.

$$f_d + N(a - 1/N)f_r > Naf_r \quad [1]$$

$$f_d > Naf_r - N(a - 1/N)f_r$$

$$f_d > f_r \quad [2]$$

Expression [2] is the traditional concept of individual selection, i.e., the trait must give the individual possessing the trait a higher relative fitness than the individuals not possessing the trait. This is portrayed in Fig. 1 by the solid line. Any point to the right of this line will be selected for by individual selection.

However, the A-trait increases the fitness of the trait-group only if:

$$f_d + (N - 1)f_r > 0$$

$$f_d > -(N - 1)f_r \quad [3]$$

Equation [3] represents the traditional concept of group selection, and is represented in Fig. 1 by the broken line. Any point to the right of (i.e., above) this line increases the fitness of the group.

Obviously, there is some overlap between Eqs. [2] and [3], that is, some traits selected for by individual selection also increase the group's fitness. The problem of group selection is to determine if and how those traits that are advantageous to the group, yet outside the realm of individual selection, can be selected for, and conversely, how those traits that are disadvantageous to the group, yet within the realm of individual selection, can be blocked.

If the deme contains more than one trait-group (i.e., there is a dispersal phase), the per capita fitness changes of the A and B types for the *deme* are respectively:

$$\frac{\sum_i Na_i[f_d + N(a_i - 1/N)f_r]}{\sum_i Na_i} \text{ and } \frac{\sum_i Nb_i[Na_if_r]}{\sum_i Nb_i}$$

These are simply the weighted averages of individual fitness changes over all the trait-groups in the deme. Each trait-group is assumed to have an equal overall density N and a_i,b_i are the proportions of the A and B types in each trait-group i.

As before, the A-type is selected for only if it has the highest per capita fitness.

$$\frac{\sum_i Na_i[f_d + N(a_i - 1/N)f_r]}{\sum_i Na_i} > \frac{\sum_i Nb_i[Na_if_r]}{\sum_i Nb_i} \quad [4]$$

$$\frac{\sum_i Na_if_d}{\sum_i Na_i} > \frac{\sum_i Nb_ia_if_r}{\sum_i b_i} - \frac{\sum_i Na_i(a_i - 1/N)f_r}{\sum_i a_i}$$

$$f_d > f_r\left[N\left(\frac{\sum_i a_ib_i}{\sum_i b_i} - \frac{\sum_i a_i^2}{\sum_i a_i}\right) + 1\right] \quad [5]$$

Eq. [5] gives the condition for selection of the A-trait in the deme. It is the same as expression [2] with the exception of the term:

$$N\left(\frac{\sum_i a_ib_i}{\sum_i b_i} - \frac{\sum_i a_i^2}{\sum_i a_i}\right) \quad [6]$$

The value of this term depends on the composition of the trait-groups. Given a single trait-group or trait-groups in which the proportions of A and B-types are identical, term [6] equals zero and Eq. [5] reverts to Eq. [2], the conditions for individual selection. If the types are completely segregated, such that any trait-group consists either entirely of A or entirely of B, then term [6] equals $-N$ and Eq. [5] reverts to Eq. [3], the conditions for pure group selection. Intermediate variation in trait-group composition yields intermediate solutions. Thus, the effect of increasing the variation in the composition of trait-groups is to push the system towards group selection. Graphically this is represented by rotating the solid line (giving the set of traits actually selected for) in Fig. 1 counter-clockwise, until it is coincidental with the broken line (arrow).

A variation greater than zero in the composition of trait-groups will be met by any stochastic process. If the placement of types into the trait-groups is randomly determined, then the variation in composition will follow the binomial distribution. In this case the expected value of term [6] is always -1 regardless of trait-group size (N) or the overall frequency of the A-type in the deme (a). Eq. [5] then becomes:

$$f_d > 0. \quad [7]$$

In other words, given a random distribution of types into trait-groups, any trait that increases the absolute fitness of the donor, ***regardless of its relative fitness*** will be selected for. Graphically, the solid line is rotated until it is coincidental with the y-axis. I am very grateful to F. M. Stewart for the proof of this, which will be presented elsewhere (the proof is not dependent on equal N in each trait-group).

If the variation in the composition of trait-groups is greater than random, term **[6]** yields values of less than -1, and altruistic traits that actually decrease the fitness of the donor can be selected for, such as alarm calls. This is also independent of A's frequency in the deme.

Kin that remain close to each other constitute one way of generating this greater than random variation (kin selection is thus a subset of this theory) but it is not the only way. Animal distributions are often found to be "patchy" or with a greater than random variation (9, 10). As one example, 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. Assume that the females enter the trait-groups at random, N to a trait-group, so that as far as the *female* distributions of A and B types are concerned, term **[6]** equals -1. Each female then lays e eggs. Term **[6]** for the *larval* trait-group composition is now:

$$eN\left(\frac{\sum_i a_i b_i}{\sum_i b_i} - \frac{\sum_i a_i^2}{\sum_i a_i}\right) = e(-1) \qquad [8]$$

i.e., the proportions remain the same but the density is raised by a factor e, and the right hand side of Eq. **[5]** becomes $f_r(1 - e)$, highly negative.

J. Maynard-Smith's (11) model of group selection is rather similar to the one presented here. He had the general concept of trait-groups, but apparently thought it was still necessary for altruistic traits to drift to fixation in some of the trait-groups for selection to occur. Genetic drift is not necessary for this model.

DISCUSSION

The process of group selection postulated here can be visualized in Fig. 2, showing two trait-groups with differing proportions of A and B types (2A). The A-trait is an "altruistic" defense behavior, such as a warning cry. While the animals are in their trait-groups, predation occurs and within each trait-group the B's fare better than the A's. However, ***considering both groups together the opposite is true, that is, the A's fare better than the B's*** (2B). This is because due to the A-trait, the trait-group with the most A's has less overall predation upon it.

Were the groups to remain in isolation this would mean nothing, and the A's would rapidly be eliminated. However, all animals leave the trait-groups (2C), each has a single offspring, and the population settles back into the trait-groups (2D). The increased proportionality of the A-type for the entire system is now realized within each trait-group, and by this process B is eliminated from the system.

Notice that this form of group selection never really violates the concept of individual selection. It is always the type with the highest per capita fitness that is chosen, but when the effect of more than one trait-group is considered, these are the very types that behave altruistically.

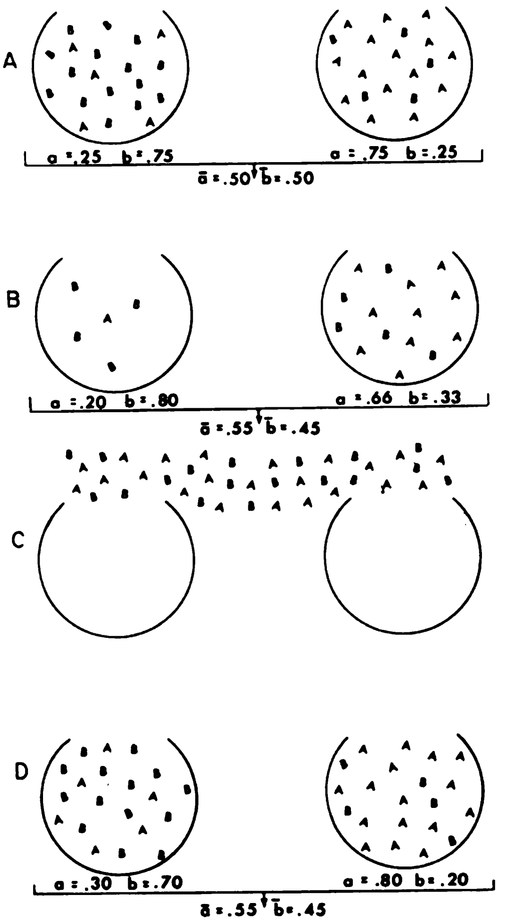

FIG. 2. Illustration of the group selection process. See *text* for explanation.

The extent to which this process of group selection occurs depends on (1) the validity of the trait-group concept, and given this, (2) the variation in the composition of trait-groups. Both may be expected to vary widely among organisms, depending on behavior and habitat. In particular, small insular habitats might constrict the deme to the size of a single trait-group and push the system towards "individual" selection; and spatial heterogeneity, by partitioning the deme spatially, may be expected to enforce trait-groups and enhance group selection. In any case, the traditional concepts of group and individual selection appear to be two extremes of a continuum, with systems in nature operating in the interval in between.

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CONCLUSIONS

What are the implications of this model, if true? The concept of structured demes admits the routine evolution of weak altruism, but at its strongest it becomes conceptually identical to kin selection. In other words, it cannot explain the evolution of any trait that could not also be explained by kin selection, but it does enlarge the number of situations in which such traits evolve.

It is also possible that both kin selection and this model are a stronger evolutionary force than is currently believed. In fact, I believe that in focusing on the concept of altruism, the whole group selection controversy has been misplaced. The fundamental question is "do populations maximize collective fitness"--whether they do so through selfish or altruistic means is a secondary consideration. Even if the structured deme process can only select for weak altruism, its role in selecting for or against traits that have <u>neutral</u> individual selection value may well increase its potency.

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