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THE QUARTERLY REVIEW of BIOLOGY



A CRITICAL REVIEW OF THE MODELS OF GROUP SELECTION

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ABSTRACT

Group selection is defined as that process of genetic change which is caused by the differential extinction or proliferation of groups of organisms. A very large proportion of the literature pertaining to group selection consists of theoretical papers; the genetic problems of group selection have been addressed from many different mathematical viewpoints. The general conclusion has been that, although group selection is possible, it cannot override the effects of individual selection within populations except for a highly restricted set of parameter values. Since it is unlikely that conditions in natural populations would fall within the bounds imposed by the models, group selection, by and large, has been considered an insignificant force for evolutionary change.

*These theoretical conclusions and the assumptions from which they have been derived are re-examined in the light of recent empirical studies of group selection with laboratory populations of the flour beetle, *Tribolium* (Wade, 1976, 1977). It is shown that the models have a number of assumptions in common which are inherently unfavorable to the operation of group selection. Alternative assumptions derived from the empirical results are suggested and discussed in the hope that they will stimulate further theoretical and empirical study of this controversial subject.*

INTRODUCTION

GROUP SELECTION is defined as that process of genetic change which is caused by the differential extinction or proliferation of groups of organisms (Wright, 1945; Wynne-Edwards, 1962; Maynard Smith, 1964; Williams, 1966; Lewontin, 1970; Wade, 1976). These groups may be any unit of population structure ranging from families (kin selection) to whole populations (interdeme or interpopu-

lation selection). [In keeping with this genetical definition, I will not directly consider selection between species (Van Valen, 1975) or between ecosystems (Dunbar, 1960), both of which have been called group selection. Although the general principles of genetical variation and heritable fitness differences would apply to selection at these levels of organization, many of the other concepts discussed, such as non-additive components of variance and gene flow, clearly would not.] The gene-frequency changes caused by group selection (as is also true for

individual selection) consist of changes in the genetic composition of individuals within populations. Individual selection requires genetic differences between individuals; group selection requires, in addition, that there be genetic differences between the units of population structure. Besides this between-group variation, the ecological processes of extinction, dispersion, and colonization are of primary importance in evaluating the role of population structure in evolution.

It is important to emphasize that both group selection and individual selection are *processes* which can change gene frequencies. They differ in the mechanism whereby gene-frequency changes are produced. As processes, group and individual selection may operate in the same direction or in opposite directions to change gene frequencies. Alternatively, one process can occur without the action of the other.

A very large proportion of the literature concerned with group selection consists of theoretical papers. Several authors, among them Maynard Smith (1964), Levins (1970), Eshel (1972), Boorman and Levitt (1973), Levin and Kilmer (1974), D. S. Wilson (1975, 1977), Gadgil (1975), Charnov and Krebs (1975), Gilpin (1975), Matessi and Jayakar (1973, 1976), and Cohen and Eshel (1976), have addressed the genetic problems of group selection from various, and sometimes divergent, mathematical viewpoints. Although all of the models have shown that group selection is possible, the general conclusion has been that selection *between* groups cannot override the effects of individual selection *within* groups except for a highly restricted set of parameter values. Since it is unlikely that conditions in natural populations would fall within the bounds imposed by the models, group selection, by and large, has been considered an insignificant force for evolutionary change (Williams, 1966; Slobodkin, 1974; Alexander, 1974; Ghiselin, 1974; Maynard Smith, 1976; Weins, 1976). Indeed, the general rule of thumb used by most ecologists and theorists at the present time is the "principle of parsimony" suggested by Williams (1966): if the evolution of an adaptation can be explained by individual selection there is no need to invoke group selection. Those authors taking exception to this general view (Levin and Kilmer, 1974; D. S. Wilson, 1975, 1977) have argued primarily that the theoretical conditions

favorable to group selection occur more frequently in nature than has previously been believed.

However, these theoretical conclusions and the assumptions from which they have been derived can be re-evaluated in the light of recent empirical studies of group selection with laboratory populations of the flour beetle, *Tribolium* (Wade, 1976, 1977). This review will examine the major theoretical contributions to the discussion of group selection, and certain of the underlying assumptions of each model will be considered in some detail. It will be shown that, in addition to the many assumptions which are unique to any specific model, the models in general have a number of assumptions in common which are inherently unfavorable to the operation of group selection. Alternative assumptions derived from the empirical studies are suggested.

It is not my intention in this review to advocate group selection as a major force for evolutionary change, but rather to stimulate further theoretical and empirical inquiry into this controversial subject. For this reason, the discussion will be concerned with group selection as a *process*, and it will not focus on group selection as an *explanatory principle* for the evolution of particular traits in natural populations. Just as the utility of a model lies in its potential ability to suggest new avenues of experimentation, empirical observations can provide grounds for modifying prevailing theoretical opinion (cf. Mertz, Cawthon, and Park, 1976, for a recent example). Because of the recent expansion of theory in ecology and population biology, a close interaction between theory and experiment is not only desirable but necessary for understanding the genetical and ecological processes governing evolution in natural populations.

General Assumptions of the Models of Group Selection

Extinction, dispersion, and colonization are essential features of any model of group selection. The extent to which group selection can influence gene frequencies is determined by the interaction of these three processes. In particular, several different modes of extinction and dispersion are possible; each has different effects on the distribution of selective forces

within groups, the amount of genetic variation between groups, and the "heritability" of genetic traits at the group level. All of the theoretical attempts to describe group selection mathematically have made assumptions concerning extinction, dispersion, and colonization which were considered biologically realistic by the authors and which served to reduce a formidable problem to more tractable proportions.

On the basis of those assumptions, the models of group selection can be classified into two broad categories depending upon the paradigm of population structure employed. One set of models can be called the *traditional group*, since they are essentially analytic approximations of Sewall Wright's shifting balance theory of evolution (Wright, 1929, 1931, 1932, 1945, and, more recently 1977). The traditional models assume that the species consists of many randomly mating local populations that are genetically interconnected by some small number of dispersing individuals at each generation. In these models gene frequencies can be altered by the differential extinction and recolonization of these partially isolated local populations. The models by Wright (1945), Maynard Smith (1964), Levins (1970), Eshel (1972), Boorman and Levitt (1973), Levin and Kilmer (1974), and Gilpin (1975) fall into this category of traditional models.

The second category of group selection models can be labeled the *intrademic group*. These models postulate a single panmictic population whose members are distributed into isolated neighborhoods or "trait groups" (sensu D. S. Wilson, 1975, 1977) during some stage of development. The interactions between individuals within the trait groups result in viability differences between the members of the different groups. Differently put, the genotypic composition of a trait group determines the viability of its members. Owing to these viability differences, some trait groups make a larger contribution of individuals to the mating pool than do others. Thus, group selection in these models occurs by the differential dispersion of the trait groups. The models in this category are those of D. S. Wilson (1975, 1977), Gadgil (1975), Charnov and Krebs (1975), Cohen and Eshel (1976), and Matessi and Jayakar (1973, 1976). The models of kin selection (Hamilton, 1964a, b) represent a special case of the intrademic models in which the trait groups or

neighborhoods consist of related individuals (see D. S. Wilson, 1977, or Charnov, 1977, for mathematical proof of this equivalence).

The models in both groups share some or all of the following five assumptions, which will be discussed seriatim:

- (1) It is assumed that the frequency of a single allele within a population can produce a significant change in the probability of survival of that population, or in the genetic contribution which the population makes to the next generation.
- (2) All populations contribute migrants to a common pool, called the "migrant pool" (Levins, 1970), from which colonists are drawn at random to fill vacant habitats.
- (3) The number of migrants contributed to the migrant pool by a population is often assumed to be independent of the size of the population. Thus, the frequency of an allele in the migrant pool can be represented by the mean allele frequency of all contributing populations.
- (4) It is assumed, often implicitly, that the variance between populations (which is a prerequisite for the operation of group selection) is created primarily by genetic drift within the populations and, to a lesser extent, by sampling from the migrant pool.
- (5) Group and individual selection are assumed to be operating in opposite directions with respect to the allele in question. In short, the allele is favored by selection between groups but disfavored by selection within groups.

A theoretical framework is specified by these postulates and group selection is constrained a priori to operate within the given limits of the models. The models to be discussed and their attendant assumptions are presented in Table 1, which will be referred to from time to time in the text. In the sections to follow, the effects of each of these five assumptions upon the process of group selection are discussed, and alternative assumptions that can be derived from the empirical results (Wade, 1976, 1977) are suggested.

ASSUMPTION 1: SELECTION ON A SINGLE LOCUS

Theoretical inquiry into group selection has been mainly concerned with clarifying the con-

ditions under which a single allele can increase in frequency by means of group selection when that allele is disfavored by individual selection (cf. Table 1, column 1). Deterministic models of selection on a single locus are standard practice in population genetics theory and are a direct and reasonable approach to many genetic problems. Several genetical aspects of natural populations important to the process of group selection, however, cannot adequately be discussed in the simplified context of such models. These are, namely, genotype-genotype interactions, epistatic effects between loci, and local variation in the direction and intensity of individual selection.

The strong effect of the biotic environment on fitness by means of genotype-genotype interactions has been abundantly demonstrated empirically (Wright and Dobzhansky, 1946; Lewontin, 1955; Levene, Pavlovsky, and Dobzhansky, 1954; Lewontin and Matsuo, 1963; Sokal and Huber, 1963; Sokal and Karten, 1964; Ehrmann, 1966, 1967, 1968; Spiess, 1968; Bryant, 1969, 1970; Bryant and Turner, 1972; Taylor and Sokal, 1973), and epistatic effects are demonstrated by most alleles which have been investigated in different genetic backgrounds (e.g., Wright and Dobzhansky, 1946; Wright, 1949; Wallace, 1968; Sokal et al., 1974; McCauley, 1977). Spatial variation in

TABLE 1
The models of group selection and their assumptions

AUTHOR	SINGLE LOCUS (1) OR ALTERNATIVE PHENOTYPES (2)	MECHANISM OF GROUP SELECTION: EXTINCTION (E) OR MIGRATION (M)	MIGRANT POOL	ORIGIN OF BETWEEN-GROUP VARIATION	GROUP VS. INDIVIDUAL SELECTION*
<i>Traditional Models</i>					
Wright (1945)	1	E	+	genetic drift	+
Maynard Smith (1964)	1	M	+	genetic drift	+
Levins (1970)	1	E	+	genetic drift, sampling error	+
Eshel (1972)	2	E	Intermediate ^a	genetic drift	+
Boorman and Levitt (1973)	1 ^b	E	+ ^c	genetic drift	+
Levin and Kilmer (1974)	1	E	+	genetic drift	+
Gilpin (1975)	1	E	+	genetic drift	+, (-) ^d
<i>Intrademic Models</i>					
Wilson (1975, 1977)	1	M	+	sampling error ^e	+, (-) ^d
Gadgil (1975)	1	M	+	(unclear)	-
Charnov and Krebs (1975)	2	M	+	sampling error	+
Matessi and Jayakar (1973, 1976)	2	M	+	sampling error ^e	+
Cohen and Eshel (1976)	1	M	+	sampling error	+

*+ indicates that the assumption is a part of the structure of the model; - indicates that the assumption is not a part of the model.

^aThe model can consider the effects of a migrant pool, a propagule pool, or an intermediate form of colonization by adjusting parameter values.

^bA two-locus model is outlined but not developed.

^cInstead of a migrant pool, the model assumes that a larger stable source of migrants exists independent of the local demes. This structure is mathematically equivalent to the migrant pool.

^dGroup selection and individual selection acting in the same direction are discussed, although not analytically considered.

^eThe sampling error can be enhanced by non-random assortment into trait groups on the basis of phenotype or kinship.

selection pressures has also been reported frequently in both laboratory and field studies, and it can often be related to environmental variation in microhabitats (e.g., Gordon, 1935; Dobzhansky, 1948; Selander, Hunt, and Yang, 1969; Koehn and Mitton, 1972; Koehn, Milkman, and Mitton, 1976).

These multivarious effects of the same allele when in different genetic backgrounds or different local habitats can result in continual change in both the direction and the intensity of individual selection. Depending upon the initial genotypic composition of the population, individual selection could result in the attainment of any of a number of different gene frequencies corresponding to local "adaptive peaks" (Wright, 1956). Although the particular gene frequency attained may not be the optimum when all possible genotypes are considered, individual selection within the population would prevent a shift from the local peak to the optimum. The net result is a "multiplicity of adaptive peaks on a selection surface" (Wright, 1931, 1956, 1959), with no single gene or gene frequency conferring more than a temporary or local advantage. Individual selection itself would contribute to the genetic variation between populations.

That is, to the extent that individual selection pressures vary in sign or magnitude among local populations—owing to frequency dependence, density dependence, epistatic effects, or combinations of these—individual selection will act to generate and maintain genetic differences among the local populations. This could occur, as indeed it has been shown in many of the experiments cited above, even in the absence of conspicuous environmental variation among the local habitats. Thus, even in those cases where the net effect of individual selection is opposite to that of group selection, temporal and spatial variation in the components of selection at the individual level can assist the opposing process of group selection by contributing to the amount of variation between populations.

In contrast, the group selection models examine populations which are genetically subdivided but experience a uniform selective environment. In such populations individual selection upon alleles at a single locus (in the absence of heterosis, which is not treated by the

models) can operate only to increase or decrease gene frequencies in a deterministic way. The models postulating alternative phenotypes (cf. Table 1) without specifying the underlying genetic system are no more realistic in this respect. Because of this, Wright's concept of a multiplicity of adaptive peaks on a selection surface is not applicable in the context of the group selection models, and several of the potentially important forces for creating genetic variation between populations have been omitted from previous theoretical work. Multiple loci were considered briefly in outline by Boorman and Levitt (1973) in their model of group selection among small populations at the border of a larger stable population. They assumed, however, that the individual genetic processes within the boundary populations were negligible relative to the time scale of extinctions, and thus they excluded an important feature of the two-locus case from their analysis.

In addition to the above-mentioned genetical phenomena, models of group selection on a single locus are lacking in a second respect. Many such models postulate that the frequency of a single allele could affect the probability of extinction or proliferation of an entire population, whereas group selection is more likely to be involved in the evolution of polygenic characters and characters which are emergent properties of populations, such as population density (Wright, 1931; Wynne-Edwards, 1962; Boorman and Levitt, 1973; Gilpin, 1975).

Data which are available tend to support this polygenic hypothesis. Group selection for increased or decreased population size at 37-day intervals in *Tribolium* (Wade, 1976) resulted in significant and simultaneous changes in several of the primary characteristics known to affect population size (for recent reviews see King and Dawson, 1972; Mertz, 1972; Sokoloff, 1974), namely, fecundity, fertility, body size, developmental time, and various cannibalistic pathways. Furthermore, measurement of the between-populations variance for each of these characters indicated that different populations within the same group-selection treatment had responded in different ways (Wade, 1976). Theoretical studies of selection on a single locus are not likely to contribute insights into such genetically complex processes!

Models of selection on quantitative characters

which assume an underlying polygenic mode of inheritance, such as the models of Bossert (1963), Slatkin (1970), Slatkin and Lande (1976), and Lande (1976), may be more appropriate to the theoretical study of group selection. This type of model permits a more realistic description of the effects of selection on quantitative traits with respect to the genetic variance between and within populations. Specifically, the mean values of a trait among local populations can be varied independently of the within-populations variance of that trait. This is different from the single-locus case, where the variance is a function of the gene frequency. Laboratory selection experiments have shown that directional selection among individuals can bring about large changes in the mean value of a quantitative character without substantially altering the variance (Robertson and Reeve, 1952; Tantawy and Tayel, 1970). Although the additive components of the variance generally decline under selection, the epistatic components which can contribute to the variance between populations are often increased. This is important because selection *within* populations depends upon the additive components of the genetic variance, whereas selection *between* populations depends upon the total genetic variance.

ASSUMPTION 2: THE MIGRANT POOL

The term "migrant pool" was introduced into the discussion of group selection by Levins (1970), and all of the earlier and later models employ mathematically equivalent structures (cf. Table 1). This concept is useful from a mathematical point of view, since it permits a simple and straightforward analytical treatment of the process of colonization. The expected value of the gene frequency in habitats newly colonized by dispersing individuals is equal to the frequency in the migrant pool. Also, the frequency in the migrant pool is the average frequency of the surviving populations.

The migration of individuals between populations and the colonization of new or vacant habitats have not been systematically studied in natural populations, but certain general and relevant features of the dispersion process may be inferred. From a biological point of view, a migrant pool implies a population structure in

which migrants from any one population are as likely to colonize a vacant habitat as migrants from any other population. Differently put, whatever population structure exists, that structure in no way constrains migrating individuals. This assumption, although biologically realistic for the intrademic models, is quite unrealistic for the traditional models. With the possible exception of benthic fauna with pelagic larvae or, perhaps, those plant species with wind-dispersed seeds, it is not likely that natural populations of most other organisms have the population structure specified by the traditional models. Indeed, geographical barriers to migration as well as behaviorally restricted movement patterns are believed to interact with and give rise to population structure.

Besides restricting the biological scope of the traditional models, the assumption of a migrant pool is extremely unfavorable to the operation of group selection in both types of models in certain additional respects. These are discussed separately in the next two sections.

ASSUMPTION 3: MIGRATION AND POPULATION SIZE

If all populations are assumed to contribute equal numbers of migrants to the migrant pool—as is often done in the traditional models (cf. Table 1)—then the gene frequency in the pool is the average frequency of all the contributing populations. With such an assumption, however, there is no possibility of group selection by means of the differential proliferation of populations.

For example, let population N_1 contain 20 haploid individuals, of whom 4 carry the gene A and 16 the gene B . The frequencies of A and B in N_1 are, respectively, 0.20 and 0.80. Let a second population, N_2 , consist of 100 individuals and let the frequency of A in N_2 equal 0.90 and B equal 0.10. If N_1 and N_2 contribute equally to the common pool of migrants, the frequencies of A and B in the migrant pool are simply:

$$[A] = (0.20 + 0.90)/2 = 0.55 \quad (1)$$

and

$$[B] = (0.80 + 0.10)/2 = 0.45. \quad (2)$$

However, if the populations each contribute some equal proportion, p , of their numbers to

the migrant pool, then the frequencies in the pool are the weighted average frequencies:

$$[A] = \frac{(20)(p)(0.20) + (200)(p)(0.90)}{(20 + 200)(p)} = 0.84 \quad (3)$$

and

$$[B] = \frac{(20)(p)(0.80) + (200)(p)(0.10)}{(20 + 200)(p)} = 0.16. \quad (4)$$

Thus, the differential contribution of populations on the basis of size can have a significant effect upon the composition of the migrant pool. This is the mechanism responsible for the genetic changes observed in the intrademic models, but it has been ignored in the traditional models.

On the other hand, the intrademic models generally assume that the initial sizes of the trait groups are equal and constant (but see Matessi and Jayakar, 1976; and Cohen and Eshel, 1976). Differential viability within the trait groups owing to the genotypic composition then results in some groups being larger than others at the time of mating. It is possible to increase the intensity of group selection in the intrademic models by making a somewhat different assumption. It can be shown that, if initial group size and gene frequency are correlated, equation (3) of D. S. Wilson (1975),

$$f_d > f_r(1 - N) \quad (5)$$

becomes

$$f_d > f_r(1 - \bar{N} - \text{Cov}(N_{Ai}, N_i)/\bar{N}_A) \quad (6)$$

where f_d is the fitness change of an individual performing a certain behavior; f_r , the fitness change to the individual receiving the behavior; N_{Ai} , the number of A individuals in population N_i ; \bar{N} , the average population size; and \bar{N}_A , the average number of A individuals per population.

The ratio f_d/f_r must exceed the quantity $(1 - N)$ in Wilson's model in order for group selection to override successfully the effects of individual selection within groups. However, it is clear from expression (6) that, when population size is positively correlated with gene frequency, this condition is relaxed by an amount proportional to the covariance (Cov) between the number of A individuals, N_{Ai} , and the size of the groups, N_i .

It can reasonably be argued that in many

cases group size should be positively correlated with other traits also undergoing group selection. Consider two groups of identical genotypic composition which differ in initial size. If the viability within the trait groups is a function only of gene frequency, then the larger group will make a larger contribution to the randomly mating pool. To the extent that the difference in size is genetically determined, group selection will favor large initial trait-group size. In addition, since the viability differences are the result of interactions between individuals, it must often be the case that the effects of these interactions increase with increasing density.

These effects of variable group size were considered by Matessi and Jayakar (1976), who found that group size was a "critical factor" only when the within-group fitnesses were a function of the frequency of altruists, and not when they were a function of the numbers of altruists. However, in examining the effects of numbers they considered a case in which the number of altruists was uncorrelated with group size, a situation which is different from the kind of density dependence suggested.

My own experimental studies of group selection (Wade, 1976, 1977) have empirically demonstrated that group selection can occur by the differential proliferation of populations in the absence of differential extinctions. The "random extinctions" treatment ("D") of Wade (1976, 1977) consisted of 48 populations, each population having been founded with a propagule of 16 adult beetles chosen at random from a laboratory stock culture. At each 37-day interval or generation thereafter, a table of random numbers was used to determine which populations would become extinct and which ones would survive. Thus, group selection by the differential extinction of populations was by design not possible in this treatment.

Extinct populations were subsequently recolonized by selecting propagules at random from those populations which, by chance, had survived the extinction process. According to plan, more propagules were taken from large populations than were taken from small populations. This differential proliferation of populations on the basis of size was continued for 233 days, or nine generations. The results demonstrated a significant increase in the average density of populations so treated, relative to the average

density in a control population in which group selection could not operate. During the last three generations of the experiment, population size in the populations subjected to random extinctions and differential proliferation exceeded that of the control populations by an average of 23 adult beetles per population (range of population size for the control was from 49 to 106 adults per population). This represents an average difference in population size of 30 per cent ($P < 0.001$).

This discussion has focused for the most part on the group-selective effect of differential proliferation on the basis of population size. Although population density is known to affect the emigratory rate of several species (Strecker, 1954; Sakai et al. 1958; Ziegler, 1976), it should be noted that any other factor that differentially influences migration could also result in group selection.

ASSUMPTION 4: THE ORIGIN OF VARIATION BETWEEN POPULATIONS

The traditional models discussed above assume that the variation between populations necessary for group selection is created primarily by genetic drift within the semi-isolated subgroups. The intrademic models assume that the necessary variation arises in the sampling of colonists from the migrant pool. It is useful to separate these two types of sampling error because they represent two different biological processes, which usually occur at two very different stages in the life history. These theoretical assumptions regarding the origins of between-populations variance are responsible in large part for the conclusion that group selection is not likely to be a significant force for evolutionary change in natural populations.

The traditional models specify several necessary conditions for the operation of group selection, namely, small group size, low levels of intergroup migration, and weak individual selection within groups. These limitations are identical to those for which genetic drift is important to the differentiation of local populations. The intrademic models also require small initial group size in order to create a large between-group variance when sampling from the migrant pool. It is clear that the results of both models are strongly dependent upon the mechanisms which give rise to genetic variation

between populations. Moreover, the potential amount of variance between populations is limited by the migrant pool per se for reasons which are explained hereafter. Natural populations are not likely to lie at either of the extremes represented in Fig. 1, but discussion of the effects of these possibilities serves two purposes. First, all of the group selection models but two (cf. Table 1) employ either a migrant pool or a "propagule pool"; and, second, an understanding of these two extreme cases can provide insight into the more intermediate processes of colonization.

If colonists are chosen at random from the migrant pool, the gene frequencies of the newly colonized populations will be normally distributed about the mean of the migrant pool. Specifically, these populations will have an expected gene frequency equal to that of the migrant pool; the genetic variance among them will be equal to the variance of the migrant pool divided by the size of the sample or colonizing propagule. (It will be recalled from section 3 that the mean of the migrant pool is simply the average frequency of populations contributing migrants for many of the models.) A portion of the genetic variance between populations is lost because of migration at each generation. The genetic variance must therefore be regenerated by the sampling process at each colonizing episode if group selection is to be effective. If the genetic variance between populations is not renewed, the process of group selection will come to a halt. Uniform and directional individual selection operating within each local population or trait group will also tend to decrease the sampling variance from the migrant pool. In addition, owing to the extensive mixing of individuals from different populations, the migrant pool greatly reduces the correlation or "heritability" of traits between group and propagule. (This aspect of the migrant pool will be discussed in greater detail below.)

The effects of the migrant pool are most extreme in the intrademic models of group selection. In this case the migrant pool is a single panmictic population from which individuals disperse at random into isolated groups at some other stage in the life history. Thus, extensive mixing occurs at every generation.

An alternative mode of recolonization was employed in my experimental studies of group

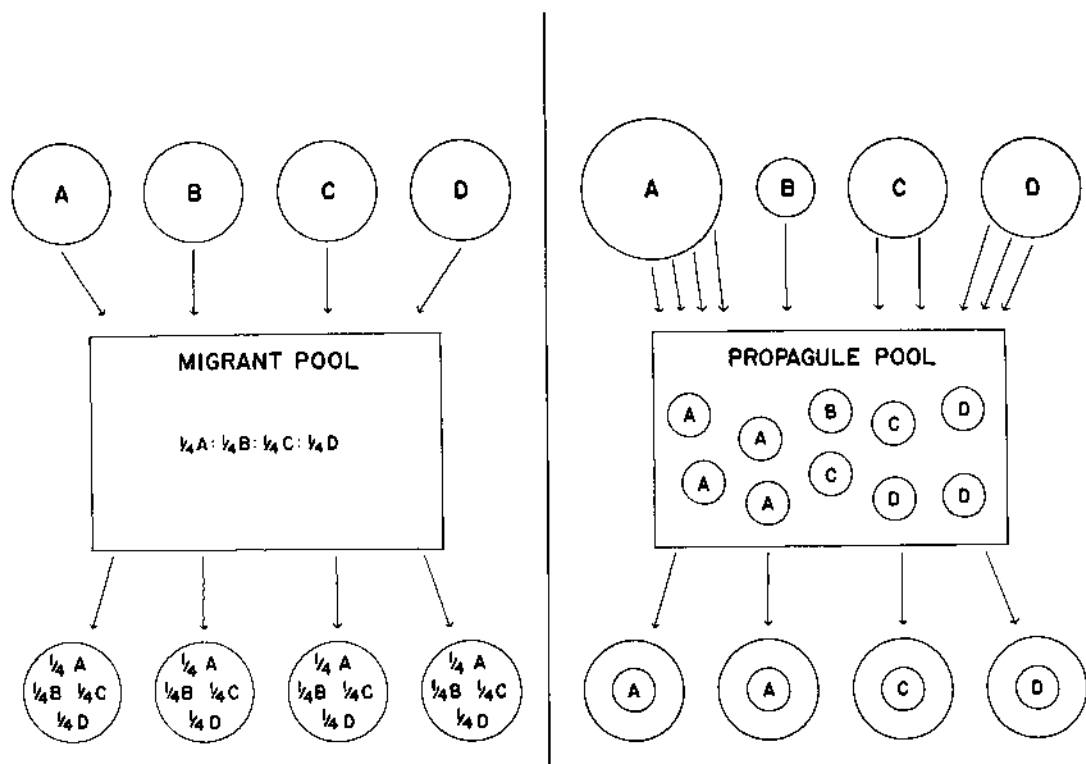


FIG. 1. THE DIAGRAM ILLUSTRATES THE DIFFERENCES BETWEEN THE CONCEPTS OF A MIGRANT POOL AND A PROPAGULE POOL

See text for further explanation.

selection (Wade, 1976, 1977). Groups of colonists were chosen at random directly from *each* population, and one new population was established with each such propagule. Therefore, according to the experimental design, migrants were chosen from a "propagule pool" instead of a migrant pool, and no mixing of colonizing individuals from different populations was permitted to occur.

In the absence of selection, it can be shown that this mode of colonization has an effect on the between-populations variance which is very different from the effect of the migrant pool. The equilibrium variance between populations is greater for the case of the propagule pool by an amount proportional to the ratio of the extinction rate to the sum of the migration and individual selection rates (Slatkin and Wade, *in press*). In my own empirical studies (Wade, 1976, 1977), this process of random extinctions with recolonization from a propagule pool was

observed to convert a large proportion of the total variance in population size into the between-populations component of the variance. It was pointed out that this process "... will establish the ideal and favorable conditions for group selection to occur. In this way group selection need only be a sporadic event in nature and still accomplish large genetic change."

The differences between the concepts of the migrant pool and the propagule pool are illustrated schematically in Fig. 1. The letters *A* through *D* in this figure represent population phenotypes. The differences to be noted are the following:

- (1) the differential contribution of populations to the propagule pool on the basis of population size;
- (2) the propagules' persistence as distinct units in the propagule pool, unlike the mixing that takes place in the migrant pool;

- (3) propagules drawn from the migrant pool result in populations with identical genetic composition, whereas new populations founded from the propagule pool are genetically heterogeneous; and
- (4) the founding of populations by propagules from the propagule pool is followed by a period of population growth, whereas populations colonized from the migrant pool of the models are established at the carrying capacity of the habitats.

The different effects of the migrant and propagule pools on the process of group selection are analogous to the different effects of blending and particulate inheritance on individual selection. To explain: in a randomly mating population with blending inheritance, the average value of a quantitative trait among the offspring of a given mating is equal to the parental average of that trait. It can be shown that the variance of the population is thus reduced by a factor of one half at each generation (Fisher, 1930). For this reason, a large amount of new variation must be generated in each generation if individual selection is to be effective in producing evolutionary change under blending inheritance. Darwin, unaware of Mendel's results, which illustrated the particulate nature of inheritance, discussed at length many hypothetical and biologically unfounded solutions of this problem of evolution by natural selection with blending inheritance.

The complete mixing of individuals from several populations in a migrant pool can be considered a form of blending inheritance at the populational level. Just as blending inheritance reduces the variance within a population, the migrant pool reduces the variance between populations. This loss of variation between populations is the result of the tendency of new colonies to regress to the mean of the populations contributing to the migrant pool, as analogously, under blending inheritance, the offspring regress to the mean of the parental generation. Thus, group selection with a migrant pool cannot be very effective unless a significant amount of between-populations variance can be generated at each colonizing episode.

In order for colonization to create variation between populations, the size of the founding group drawn at random from the migrant pool

must be small. This follows directly from the well-known statistical fact that the variance among sample means increases as the sample size decreases. A somewhat different situation obtains in the case of the propagule pool, where propagules of intermediate size are more favorable to group selection than either large or small propagules. (It will be recalled from Fig. 1 that in the propagule pool colonists are selected at random directly from *each* population.) On the one hand, small propagule size increases the variance between propagules as it does with the migrant pool. A large propagule, on the other hand, will be a more representative sample of the population from which it was chosen, and, for this reason, the heritability of traits at the populational level (i.e., the correlation between "parent" population and "offspring" propagule) increases with increasing propagule size. Because of this trade-off between populational variation and populational heritability, a propagule pool with an intermediate propagule size is expected to be most favorable to group selection.

Another method of increasing the variation between trait groups, despite the homogenizing influence of the migrant pool, is to invoke some degree of non-random assortment of individuals into the trait groups. Clearly, this assortment must be of the positive type where "like" associates with "like," for negative assortment would make the trait groups more similar to one another and would reduce the variation below that expected on a random basis. In many of the intrademic models, most notably those of D. S. Wilson (1977) and Matessi and Jayakar (1976), various ways of achieving a positive assortment of genotypes into the trait groups are discussed.

Natural populations are not likely to lie at either of the extremes represented by Fig. 1, but, depending on the nature and the extent of migration, will lie somewhere between a migrant pool and a propagule pool. Group selection is expected to be more important wherever migration and colonization occur with little or no mixing of individuals from different populations or groups than wherever they occur with extensive and random mixing. It is generally believed, however, that even a small amount of migration is antithetical to the maintenance of genetic variation between populations which

must be present for the operation of group selection (Maynard Smith, 1964; Williams, 1966).

Maynard Smith's "haystack" model arrives at this conclusion partly as a result of the extreme nature of individual selection within groups in his model. In that model, despite the original pattern of variation among the local groups after colonization, only two alternative types of groups remain after individual selection against the altruists, namely, groups composed entirely of altruists, or groups composed entirely of non-altruists. Differently put, any group which contains even a single non-altruist will be converted by individual selection within the group to a completely non-altruistic group. Any migration between the altruistic and non-altruistic groups or any mixing of their propagules has disastrous consequences for the evolution of altruism.

Wright (1931) and Maruyama (1970) have shown, on theoretical grounds, that populations that exchange on the average one migrant every other generation will be genetically identical at equilibrium. Although this result is correct, the argument as it applies to group selection has been somewhat misconceived (Wright, pers. commun.). It is not the expected value of the gene frequency, but rather the variance about that expectation which is important for group selection. Wright (1931) has emphasized that the equilibrium variance between populations is not negligible even for moderate amounts of migration.

Furthermore, to the extent that populations are isolated by distance, migrants from populations close to one another are more likely to disperse to the same area than are migrants from distant populations. Just as assortative mating can retard the rate at which individual variation is lost under blending inheritance (Fisher, 1930), migration "assortative by distance" will modify the effects of mixing in the migrant pool.

ASSUMPTION 5: GROUP AND INDIVIDUAL SELECTION IN OPPOSITE DIRECTIONS

Wynne-Edwards (1962) has suggested that individual selection within populations generally tends to increase population size and that this tendency is opposed by the extinction of

large populations because of an overexploitation of resources. It is also likely, however, that propagule number is often proportional to population size in many cases of biological interest, and group selection could thus favor increased productivity. Although it is clear that group and individual selection could operate in the same direction with respect to a particular trait, this possibility has rarely been considered (cf. D. S. Wilson, 1975; Gadgil, 1975). Indeed, Williams' advocacy of parsimony states that if the evolution of a trait can be explained by individual selection there is no need to invoke group selection. The use of this widely adopted principle clearly restricts the discussion of group selection to those cases in which it operates in a direction opposite to individual selection. Most of the models in Table 1 explicitly or implicitly assume that group and individual selection are opposing forces, and the theoretical discussion has focused mainly on the evolution of those traits for which the levels of selection are in conflict.

Any trait which directly or indirectly decreases the likelihood of extinction or increases the likelihood of the successful proliferation of populations will be favored by group selection. If that same trait enhances the survivorship or reproductive success of individuals within populations, then individual selection will also favor that trait. In such a case, the rate of gene frequency change is expected to be greater than the rate of change when either group or individual selection is acting alone.

In the "Control Treatment" (C) of Wade (1976, 1977), individual selection was observed to change the mean population size at day 37 from greater than 200 adults per population in generation one to less than 50 adults per population in generation nine. Group selection for decreased population size was also studied in a second treatment (B). A comparison of the two treatments permits an evaluation of the effect of group and individual selection acting *together* relative to the effect of individual selection acting alone. Population size at day 37 changed much more rapidly in the B Treatment; the mean population size in this treatment was less than *half* of the Control mean during the last four generations of the experiment ($P < 0.0001$).

When further experiments were conducted

to determine the cause of the decline in population size in both treatments, another significant and surprising difference was discovered. Individual selection in the populations of the Control Treatment had caused an increase in the cannibalism rate of adults feeding on pupae and a small but significant increase in the developmental time of males and females relative to the group-selected populations. (Wade, 1976). In contrast, populations from that treatment (B) where both group and individual selection had favored small population size responded in a more heterogeneous fashion. In some of those populations cannibalism rates had increased significantly while fecundity remained unchanged, and in other populations developmental time had been lengthened while fecundity had increased. Many other traits exhibited this same between-populations heterogeneity in the B Treatment (Wade, 1976). Thus, not only was the rate of change accelerated when group and individual selection were operating in the same direction, but also the genetical nature of the outcome was fundamentally different.

This new aspect of group selection has not been studied theoretically or considered seriously.

CONCLUSION

In the preceding discussion the assumptions underlying the models of group selection have been presented and evaluated. My own empirical studies of group selection on laboratory populations of *Tribolium* have indicated several biologically realistic ways in which these as-

sumptions can be modified and made more favorable to the process of group selection. Additional laboratory studies of the group selection process are currently underway and examine the effects of migration, propagule size, and extinction rates, separately and in combination, along the lines suggested. It remains for these ecological processes and their effects to be systematically studied in field populations.

I believe that when the process of group selection is more clearly understood, a more realistic evaluation of its utility as an explanatory principle for evolution in natural populations will be possible.

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