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THE GROUP SELECTION CONTROVERSY: History and Current Status

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Introduction

The study of group selection has had a remarkable history. Prior to 1966 it was a widely accepted concept, supported by some of the most prominent evolutionists of the day. It also had many prominent critics but, as with most major controversies, both sides threatened to persist indefinitely. Then, with the publication of Williams's *Adaptation and Natural Selection* (82), the concept of group selection was discredited. The fatal blow came, not from a crucial experiment, or even from a new theoretical development, but simply from the elegance and clarity of Williams's thought in interpreting developments of the previous three decades.

For the next decade, group selection rivaled Lamarkianism as the most thoroughly repudiated idea in evolutionary theory. Then it mysteriously rose from the dead. The modern version of group selection is supported by a variety of internally consistent and biologically plausible models. M. J. Wade and his associates (23, 59, 75, 76, 81) claim to have demonstrated it in the laboratory. R. K. Colwell and I (21, 22, 92) assert that biased sex ratios illustrate its operation in nature. As one author of a recent book review described the current status of group selection (68), "decent folk can again discuss it as a viable mechanism." The choice of words aptly expresses the charged atmosphere that has surrounded the subject from the beginning.

This review attempts to place the modern concept of group selection within its historical context. A historical perspective is important for several reasons. First, group selection is a fascinating example of how scientific questions arise from unscientific attitudes, and of how their development is often haphazard and unsystematic. Second, much of the recent debate over group selection

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centers around the semantic question of whether these new models should, in fact, be called group selection. This question cannot be answered without an appreciation of history. Third, even though the modern concept of group selection lies squarely within the older tradition, fundamental differences do exist that must be emphasized. Finally, one of the most striking features of the "new" group selection is its relation to other major concepts, such as inclusive fitness, game theory, and reciprocity. In the past these have been treated as rival theories, with every effort being devoted to accentuating their differences. Now it is apparent that they can be united within a single framework and that far more is to be gained by emphasizing their similarities. This change in itself is a development whose history is worth tracing.

The Verbal Tradition

Discussions of group selection today center around the mathematical representation of the subject, which began with Sewall Wright (95). Most models, however, are attempts to clarify a more nebulous, preexisting verbal idea. Since no model captures the complexity of an intuitive notion, and since the people responsible for that notion have not always read or understood the mathematical models, there are actually two separate traditions that are only partially connected to each other. In the case of group selection, the verbal tradition can be traced far back to general notions of what constitutes adaptation. These ideas do not stem from any deep understanding of nature, but rather from attitudes about human society. No one has stated this fact better than Williams (82) himself.

> There is one respect, however, in which there is general agreement. Always when biotic adaptation is postulated, its immediate or ultimate effect is the improvement of the situation from a traditional aesthetic point of view. It is assumed that: a population of vigorous individuals under heavy predator pressure is better adapted than one that is sickly and chronically starved; a population that divides its resources into stable individual territories is better adapted than one in which there is a chaotic scramble for resources; a population in which territory or social position is held by threat-display and recognition by neighbors is better adapted than one that maintains the social structure by frequent combat with effective weapons; a population with stable density, stable age distribution, etc. is better adapted than one in which such factors fluctuate widely; a population with limited fecundity and low juvenile mortality rates is better adapted than one with high fecundity and high juvenile mortality rates; a population in which old and dominant individuals regularly yield to promising youths is better adapted than one dominated by fecund but slowly displaced oligarchs; populations in which individuals, such as worker bees, often jeopardize their own well being for a larger cause are better adapted than those whose members consistently act only in their own immediate interests; those in which individuals normally live in peace or active cooperation and mutual aid are better adapted than populations in which open conflict is more in evidence; on the other hand, when active mutual destruction must take place, infanticide is preferable to the killing of peers. I submit that the only consistency found in such propositions is that they all conform to prevailing aesthetic concepts of what organisms ought to be like (82, p. 233). . . .

> There is a rather steady production of books and essays that attempt to show that Nature is, in the long run and on the average, benevolent and acceptable to some unquestionable ethical and moral point of view. By implication, she must be an appropriate guide for devising ethical systems and for judging human behavior. In some cases it would appear that "love thy neighbor" must stand or fall according to whether mutualism or parasitism is the more prevalent phenomenon. Attempts to demonstrate the benevolence of Nature often take the form of name changing. The killing of deer by mountain lions meant "nature red in tooth and claw" to a generation of "social Darwinists." To a more recent generation it has become Nature's kindness in preventing deer from becoming so numerous that they die of starvation and disease. To Darwin himself there was a poorly defined "grandeur" to such processes. The simple facts are that both predation and starvation are painful prospects for deer, and that the lion's lot is no more enviable. Perhaps biology would have been able to mature more rapidly in a culture not dominated by Judeo-Christian theology and the Romantic tradition. It might have been well served by the First Holy Truth from the Sermon at Benares: "Birth is painful, old age is painful, sickness is painful, death is painful. . . . " (82, p. 255).

I agree wholeheartedly with Williams's assessment and would like to formalize it even a bit further. Every human society is full of opportunities for some individuals to gain at the expense of others. These opportunities include cooperative activities, in which gain is not necessarily proportional to sacrifice. Assuming, for the sake of argument, that humans are motivated largely by self-interest, then those who are in a position to gain at the expense of others will be tempted to do so and those in a position to be exploited will try to prevent it. This situation automatically creates two conflicting perspectives about how humans should behave. Although both perspectives spring equally from self-interest, their expression will probably be very different, since one by definition is socially virtuous, while the other is not. Furthermore, if asserting that the exploitation of others is evil, sick, or unnatural helps to promote social virtues, then these views will certainly be expressed and defended, regardless of their factual content. The idea that selfishness is pathological should therefore be found even in societies that are governed entirely by self-interest. I doubt if this notion is confined to any religion or tradition, and I strongly suspect that it exists in all cultures. Indeed, the social climate that has surrounded the study of evolution from the beginning is probably most remarkable for its emphasis on individual selfishness (67).

The conflicting perspectives of individual selfishness vs subservience to others are so pervasive among humans that it is hardly surprising that both found their way into evolutionary thinking and were originally stated as axioms. Thus individuals, groups of individuals, species, and entire ecosystems were all endowed with purposeful, organized behavior (3, 17, 18, 26–30, 66, 97–102; see 37, 82 for additional references). Metaphorically, the larger units were compared either to single individuals (the so-called superorganism) or to highly organized human societies (with "division of labor," and so on). As Williams notes, discussions on these topics very often were merely used to buttress the attitudes that had given rise to them. Even when these discussions are ignored, however, a set of interesting and legitimate scientific questions remains. Whatever the mechanism, humans often unite into groups whose behavior is purposeful and organized and in which individual self-interest appears to be subordinated. Spectacular and unmistakable examples also exist in nature—in the social insects and in many mutualisms. In other words, group-level adaptations are a dominating feature of human life and they also exist in nature. It is as legitimate to seek their evolutionary roots as it is to investigate the roots of intelligence, learning, culture, aggression, parent-offspring relations, or any other subject pertinent to human behavior.

To this day, individual- and group-level perspectives coexist as separate schools throughout the humanities, the social sciences, and even some branches of ecology [e.g. ecosystem ecology (62, 63)]. I presume they would have coexisted within evolutionary biology were it not for the acute problem that arises when the fate of a group-level adaptation is explicitly considered. Once again, I cannot improve Williams's (83) presentation of the problem.

> Suppose that in a certain city park, of a sort suitable for the nesting of robins, the population is being regulated in the manner envisioned by Wynne-Edwards. . . . Because it is effectively regulated in relation to the food resources provided by the park, this population will never overexploit its resources and is therefore likely to survive for a long time. . . . Therefore things are going well with the robins in our park, but suppose an individual appears in which the mechanisms of reproductive restraint are absent or less well developed than is normal. In times of increased numbers, when many of the the robins are dutifully neglecting to raise a family, the abnormal bird will be among the active breeders. It will produce more than its fair share of offspring, compared to the normal birds, and the behavioral abnormality will be more abundant in the next generation. When that generation reproduces, the same thing will happen again. Selection at the individual level will cause the population to evolve a decreased level of control on its numbers. This will be true not only in one park but in all of them, and even the best controlled populations would be evolving a loss of control. Selection among populations cannot cause evolution to go in one direction, when each of the populations is evolving in the opposite direction (83, p.11).

Stated more generally, if natural selection favors individuals that leave the most offspring, then individuals that benefit themselves at the expense of others should be very fit indeed. Individuals that benefit others, presumably at some expense to themselves, would be selected against as surely as if they had bad eyes or faulty teeth. Group-level adaptations might nonetheless exist, but their evolution is hardly axiomatic. Something more is needed than the simple rules that Darwin provided.

The problem of explaining the evolution of group-level adaptations follows directly from Darwin's theory. The difficulty was not generally recognized, however, until the emerging discipline of population genetics brought it into sharp focus. Gleason (39, 40; see also 60), for example, relied mostly on the weight of empirical observations to champion an individualistic concept of plant associations in opposition to Clements's superorganismic view (17, 18).

To my knowledge, he never used the evolutionary argument that would be obvious to everyone today. Fisher (34), Haldane (42), and Wright (95), however, all emphasized that evolution within single populations could not explain group-level adaptations. Species evolving to avoid extinction and populations evolving to avoid overpopulation, require a very different mechanism than prey evolving to avoid predators. By the 1950's the superorganism school was still strong, but the need for a special evolutionary process was recognized. As Williams put it:

> It is universally conceded by those who have seriously concerned themselves with this problem that such group-related adaptations must be attributed to the natural selection of alternative *groups* of individuals and that the natural selection of alternative alleles within populations will be opposed to this development (82, p. 92).

The Mathematical Tradition

Since the primary objection to the evolution of group-level adaptations was stated in mathematical terms, a mathematical answer was required; most people looked to the work of Sewall Wright. A casual survey of major papers on group selection shows that 22 separate articles by Wright are cited. It is a curious fact, however, that only one of these articles (95) actually addresses the group selection problem, as Wright himself has recently pointed out (96). The others concern his shifting balance theory, in which a fragmented population structure is required for the selection of traits that, once evolved, are individually advantageous.

Major treatments of group selection that do not cite the appropriate paper by Wright include Wynne-Edwards's *Animal Dispersion in Relation to Social Behavior* (97), Maynard Smith's "Group selection and kin selection" (56), and Lewontin's "The units of selection" (53). I certainly do not mean to accuse these authors of poor scholarship, and will cheerfully confess my own incognizance of history below. All scientists arrive at their ideas through unique pathways, and they seldom have time completely to review an idea's history. Nonetheless, it is important to recognize that the mathematical approach to group selection is polyphyletic and did not stem solely from the earliest paper on the subject. By my own reckoning, there were at least three independent derivations prior to 1972 whose similarities and differences must be kept in mind.

WRIGHT'S CONCEPT OF GROUP SELECTION Wright (95) represented the basic problem with the single-locus model shown in Table 1. The A_1 allele codes for a "socially advantageous" character that is "of value to the population, but disadvantageous at any given moment to the individuals" (95, p. 416). The fitness of individuals carrying this allele is reduced by a factor of $(1-s)$ for heterozygotes and $(1-2s)$ for homozygotes. The fitness of all genotypes is increased by a factor $(1+bp)$, which is in direct proportion to the frequency of the A_1 allele (p). The term s therefore measures individual sacrifice, while the term b measures group benefit. It is simple to calculate changes in group size (N) and allele frequency after selection:

$$\Delta N = Np[b-2s(1+bp)] \qquad 1.$$

$$\Delta p = -sp(1-p)/(1-2sp) \qquad 2.$$

The A_1 allele increases group size whenever $b > 2s/(1-2sp)$. Equation 2 is negative, however, and implies that p will always tend towards zero. Thus the character does not evolve, even though the average individual would benefit by it.

Two aspects of Wright's model should be stressed. First, notice that the fitness of A_1A_1 and A_1A_2 genotypes can easily exceed a value of 1. In other words, the character can increase the organism's absolute fitness, yet still be selected against. Second, notice that the term for group benefit (b) does not even appear in the equation for allele frequency change. According to Wright's model, natural selection is totally insensitive to group benefit, no matter what its value. An analogy might be drawn with a person who buys a number of lottery tickets for himself and the same number of tickets for everyone else in the lottery. That person has not increased his chances of winning the lottery; if he buys more tickets for others than for himself, he will have actually reduced his chances, even though he may have a large number of tickets. Only by obtaining more tickets relative to everyone else can the person increase his chances of winning the lottery. This is nothing more than the concept of relative fitness, which forms the cornerstone of individual selection theory. In Williams's words: "Every adaptation is calculated to maximize the reproductive success of the individual, relative to other individuals, regardless of what effect this maximization has on the population" (82, p. 160).

Wright's model is an elegant formulation of the problem, but what about the solution? Wright pointed out that if many such populations existed whose frequency of the A_1 allele varied, then those with the highest frequency would grow the fastest, sending out the most dispersers to colonize new groups. In other words, the differential productivity and persistence of some groups relative to others favors the evolution of characters that increase the productivity and persistence of groups. The process is exactly analogous to the differential fecundity and survivorship of some individuals relative to others, favoring the evolution of characters that increase fecundity and survivorship of individuals within groups. Indeed, the two processes are so similar that the terms group selection and individual selection are well deserved.

Unfortunately, although Wright clearly visualized the nature of the solution, he only presented the briefest sketch of it. Major aspects of the population structure were not specified, which made it impossible to determine the relative

Table 1 Wright's (95) model for "socially advantageous" A_1 allele that benefits the group (b term) at the expense of itself (s term); the frequency of the A_1 allele is p

Genotype	Frequency	Selective value
A_1A_1	p^2	$(1 + bp)(1 - 2s)$
A_1A_2	$2p(1 - p)$	$(1 + bp)(1 - s)$
A_2A_2	$(1 - p)^2$	$(1 + bp)$

strengths of these two opposing forces. Wright merely concluded that "It is indeed difficult to see how socially advantageous but individually disadvantageous mutations can be fixed without some form of intergroup selection" (95, p. 417). Apparently, at that time the existence of such traits was not seriously questioned. Although Wright's treatment of the problem was brief and incomplete, it (and the general corpus of his work) supported speculation for another 20 years, culminating in Wynne-Edwards's (97) and Emerson's (30) extravagant claims that caused Williams (82) to write his rebuttal.

WYNNE-EDWARDS'S CONCEPT OF GROUP SELECTION Wynne-Edwards (97) did not build a mathematical model of group selection himself, but later models were so heavily influenced by his verbal account that it constitutes a second derivation.

> There are a great many important characters of this kind, not only in animals but in plants also, that are in the nature of collective attributes, all possessing the common quality of contributing to the welfare and survival of the group as such, and when necessary subordinating the interests of the individual. One of these is reproductive rate. . . .
>
> It has become increasingly clear in recent years, not only that animal (and plant) species tend to be grouped into more or less isolated populations . . . but that this is a very important feature from an evolutionary standpoint . . . .
>
> Above all, the local stock conserves its resources and thereby safeguards the future survival of its descendents; and no such conservational adaptation could have evolved if the descendants did not normally fall heirs to the same ground. Thrifty exploitation today for the benefit of some randomly chosen and possibly prodigal generation of strangers tomorrow would make slow headway under natural selection. . . .
>
> Some such local groups may in practice maintain their identity for centuries, and even, as we shall see later, for thousands of years. Others are not so fortunate and suffer a constant turnover of colonisation and extinction, especially in the less permanent types of habitat. . . . Survival is the supreme prize in evolution; and there is consequently great scope for selection between local groups or nuclei . . . Some prove to be better adapted socially and individually than others, and tend to outlive them, and sooner or later to spread and multiply by colonising the ground vacated by less successful neighbouring communities. . . .
>
> Evolution at this level can be ascribed, therefore, to what is here termed group selection—still an intraspecific process, and, for everything concerning population dynamics, much more important than selection at the individual level (97, pp. 19–20).

Wynne-Edwards's concept of group selection differed from Wright's in at least two important ways. First, Wynne-Edwards clearly emphasized highly persistent groups such as breeding colonies of shorebirds (97), although he also considered more ephemeral groups such as wood lice occupying separate tree trunks (98). Wright also envisioned multigenerational groups, but his emphasis was rather the reverse. Second, although both acknowledged the existence of many kinds of group-beneficial traits, Wynne-Edwards focused almost exclusively on population regulation. He imagined animals reproducing below their potential, so that the population does not go extinct. In contrast, the socially beneficial trait in Wright's model causes the population to grow faster, sending out more dispersers to colonize new groups. Wright therefore emphasized the differential productivity of groups while Wynne-Edwards stressed differential extinction. In retrospect, these two approaches can easily be united; groups that grow below their potential can ultimately produce more dispersers in the same way that birds who reduce their clutch size ultimately can produce more offspring. At the time, however, the difference in perspectives may have appeared more substantial.

A large proportion of group selection models clearly bears the stamp of Wynne-Edwards's ideas (4, 7–9, 11, 31, 38, 50, 52, 103; see also 73, 77). Most utilize a single-locus model with a fixed number of sites that groups may occupy. Within every group, the A_2 allele increases in frequency, ultimately becoming fixed. The probability of extinction, however, is directly related to the frequency of the A_2 allele; the relationship can be linear (e.g. 50), or it can be characterized by threshold effects (e.g. 38). When a group becomes extinct, its site is made available for colonization by dispersers from other groups. Dispersal is usually assumed to be independent of frequency. In other words, groups that are fixed for A_1 persist longer than groups containing A_2 alleles, but they do not produce more dispersers per unit time. Finally, extinction is caused only by the A_2 allele. No groups go extinct and no new sites are created by external factors.

These models have been evaluated many times (e.g. 57, 73, 77, 93, 94); the usual conclusion is that group selection is a significant force only for a narrow range of parameter values. My purpose here is merely to review the assumptions of the models.

MAYNARD SMITH'S CONCEPT OF GROUP SELECTION The publication of Wynne-Edwards's book (97) coincided with the emergence of Hamilton's inclusive fitness theory (43–45; relabeled kin selection by Maynard Smith in 56). Because both predicted the evolution of so-called altruistic behavior that benefits others at the individual's expense, Maynard Smith (56) felt the need to clarify the difference between the two theories. To do this, he built a model of group selection, only to reject it himself.

> There is one special form of group selection which is worth considering in more detail. . . . To fix ideas, suppose that there exists a species of mouse which lives entirely in haystacks.

> A single haystack is colonized by a single fertilized female, whose offspring form a colony which lives in the haystack until next year. At this time, mice migrate, and may mate with members of other colonies before establishing a new colony (56, p. 1146).

Within each haystack, Maynard Smith considered a single-locus model in which the A_1 allele at fixation produces more dispersers than the A_2 allele that displaces it. The population structure that Maynard Smith envisioned is broadly consistent with Wright's model, but it is far better specified; it differs from Wynne-Edwards's concept in at least two important ways. First, groups are not driven to extinction by the A_2 allele. Rather, all groups periodically dissolve and then form anew. Since each group's "lifetime" is fixed, the haystack model is based entirely on differential productivity, although the extinction of groups caused by the A_2 allele could easily be incorporated. Second, although there is an unspecified number of generations within each haystack, mice from all haystacks can mate during the dispersal episode. In a sense, therefore, the groups envisioned by Maynard Smith exist within a single deme. The groups envisioned by Wynne-Edwards, on the other hand, are permanently isolated; indeed, they must be if the models derived from his concept are to work.

While Maynard Smith's notion of groups was fundamentally different from Wynne-Edwards's, his haystack model also contains certain features that are puzzling in retrospect. For example, each of his groups is founded by a single fertilized female. Interactions are entirely among siblings during the first generation, among siblings and highly inbred cousins during the second generation, and so on. Many people today would regard this as an example of kin selection, yet to Maynard Smith it was an example of group selection that was specifically constructed as a contrast to kin selection. As another example, each colonizing female represents a sample of four alleles—her own diploid set plus those of her mate. To simplify the mathematics, Maynard Smith assumed that if even one of these alleles is A_2, then the entire group becomes fixed for A_2 before the next dispersal episode. In other words, selection within groups is as strong as it can possibly be. The extent to which his conclusions are an artifact of this simplifying assumption will be discussed below.

Although the three preceding versions of group selection differ in important ways, it is equally important to emphasize their similarities.

1. All of the versions consider a number of local populations that together comprise a global population. Boorman & Levitt (8, 9) consider groups on the boundary of a much larger central population, but they treat evolution only within the groups themselves.
2. All of the versions consider an altruistic [Wright's (95) term was "socially advantageous"] allele that increases the persistence and/or productivity of the group, while declining in frequency within each group. Van Valen's (74) use of the term group selection to describe the evolution of dispersal is

the only exception. Since his interesting model concerns the individual advantages of dispersal, it might profitably be relabeled.

3. Without exception, all of the models identify allele frequency change within groups as individual selection and the differential contribution of groups to the global population (whether through productivity or extinction) as group selection.
4. Without exception, all of the models assume that initially, individuals are randomly distributed into groups. Genetic differences among groups are caused by sampling error and the closely related process of genetic drift; these differences can be large only if the groups are initiated by small numbers of colonists. Genetic variation among groups can conceivably be influenced by other factors, but these models do not consider them. This oversight led Wade (77) to suggest that they are overly restrictive in their assumptions.

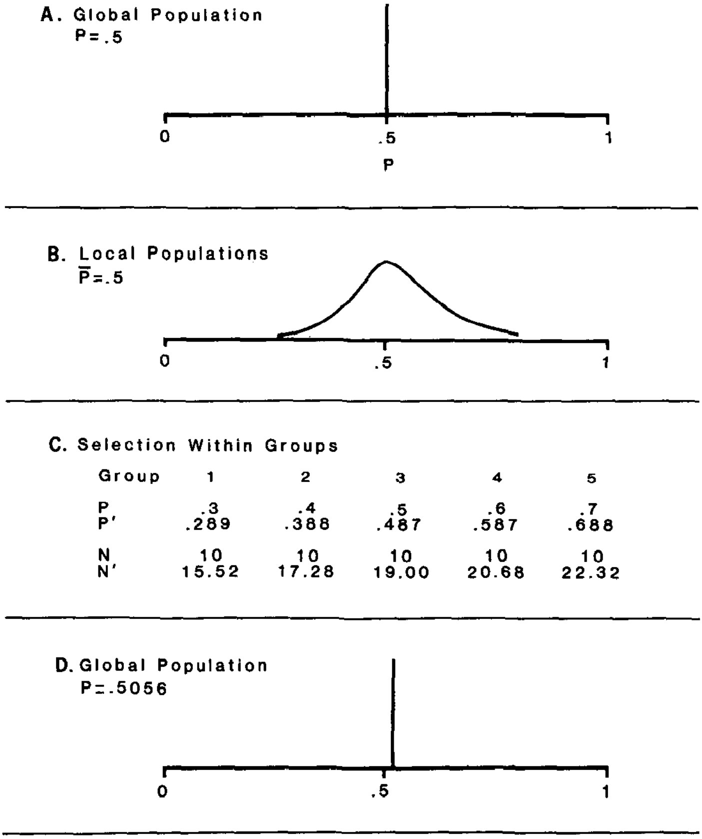
Lewontin's (53) influential paper could be considered a fourth, independent derivation of the problem. I do not consider it in detail because it does not contain a mathematical model and because it conforms closely to the common features of the three just discussed.

INTRADEMIC GROUP SELECTION MODELS Starting in 1972, another approach to group selection was independently derived no less than five times (16, 20, 54, 55, 64, 65, 85), and a substantial literature on it has arisen (6, 19, 32, 47, 69, 70, 72, 73, 80, 86–90). Although the details of the analyses differ, all of them make the same basic assumptions. A representative example is provided in Figure 1.

The model begins with a large global population and an A_1 allele at a frequency of p (p = .5 in Figure 1, Step A). Individuals then distribute themselves into local groups, much as the mice did in Maynard Smith's haystack model. The average frequency of A_1 in the groups is still $p = .5$, but p now varies among the groups, as shown in Figure 1, Step B. This variation can be random or otherwise, depending on the specific assumptions.

Selection now operates within each group. Five representative groups that vary from p = .3 to p = .7 are show in Figure 1, Step C. The A_1 allele codes for a character that increases the size of the group, but nevertheless declines in frequency within each group. The models cited above employ a variety of fitness functions; Figure 1 uses Wright's model (Table 1) with $b = 2$ and $s = .05$. The s term causes the A_1 allele to decline in frequency within each and every group (compare p' with p). The b term, however, causes group size after selection to correlate with p (compare N' to N and p).

After selection the groups dissolve, and individuals mix throughout the global population, much as in Maynard Smith's haystack model. To calculate



Group	1	2	3	4	5
P	.3	.4	.5	.6	.7
P'	.289	.388	.487	.587	.688
N	10	10	10	10	10
N'	15.52	17.28	19.00	20.68	22.32

Figure 1 Numerical example of intrademic group selection; all graphs show the relative abundance of groups (y-axis) with a given frequency (p) of the A_1 allele (x-axis). A. Global population, represented by a single frequency of A_1; B. Local groups, that vary in their p values; C. Selection within five representative groups, using Wright's model with $b=2$ and $s=.05$; D. The total frequency of A_1 from all groups in Step C, showing that the A_1 allele can evolve, even though it is selected against within each group.

the new global frequency of A_1 alleles, frequencies within each group must be weighted by group size. Since group size varies directly with p, this constitutes an evolutionary force in favor of the A_1 allele. As can be seen from Step D of Figure 1, even though the frequency of A_1 declined within every group (individual selection), the differential productivity of groups (group selection) caused it to increase slightly throughout the global population. Notice that this result is precisely what Williams (83), in the robin example cited above, asserted could not happen.

My own term for these models was structured demes (85, 87), but Wade (77) has proposed the more apt term intrademic group selection. The word intrademic emphasizes that the mixing phase incorporates all local groups into a single gene pool. With apologies for coining yet another acronym, I will hereafter shorten intrademic group selection to IGS.

The biological realism of IGS models has been discussed elsewhere (87, 90); my main goal here is to place them in the context of the group selection tradition. It should be obvious that IGS models are broadly consistent with Wright's (95) concept. In fact, they are a generalized version of Maynard Smith's (56) haystack model, in which the number of initial colonists, the genetic variation among groups, the intensity of selection within groups, the effect of the character on group productivity, and the duration of the group are all allowed to vary. They also share the common features of all group-selection models that were listed above—i.e. a number of local groups are considered, the A_1 allele is assumed to increase group size while being selected against within groups, and so on. No one familiar with the history of the subject can doubt that IGS models fall squarely within the group selection tradition.

Even more important, IGS models describe a group-level process that is strikingly analogous to individual selection. They begin with a population of groups that vary in their genetic composition. The groups also must vary in their productivity and/or persistence in a way that correlates with allele frequencies. In other words, there must be heritable phenotypic variation in group fitness. If these conditions are met, then natural selection will promote characters that increase the productivity and persistence of groups, and the rate at which these characters evolve is proportional to the genetic variation among groups. Substitute the words individual, fecundity, and survival for group, productivity, and persistence, and you have the textbook definition of individual selection. Clearly, group selection is a fully appropriate label for the IGS models.

This discussion concludes my review of the group-selection tradition. All histories are to some extent subjective, but since most of the authors cited above are still with us, I hope that they will point out any major errors I may have made. In spite of the independent derivations, there is a rough consistency among the models that makes it easy to reconcile their differences.

The Relationship Between Group Selection and Other Evolutionary Models

Any semblance of consistency disappears, however, when one attempts to trace the relationship between group selection and other important evolutionary models, such as kin selection, reciprocity, and various models that are loosely termed individual selection. These are actively studied subjects, and one might hope that the distinction between group selection and kin selection, for instance, could be specified as accurately as the differences among the various group selection models. Unfortunately, we are so far from this goal that we do not even have a consistent set of definitions. Terms such as individual selection, group selection, and altruism actually have different meanings, depending on the context in which they are used (e.g. a group selection or a kin selection model). Needless to say, this is not a sign of a mature science. In my opinion, at least two major issues must be resolved in order to make these separate branches of evolutionary ecology compatible.

LOCAL VS GLOBAL FITNESS In all group-selection models, the term individual selection refers to allele frequency change within single groups, whereas group selection indicates the differential contribution of groups to the global population. A character that is favored by group selection but disfavored by individual selection is often termed altruistic. It goes without saying that if altruistic behavior evolves by group selection, then throughout the global population the average altruist has a higher fitness than the average nonaltruist. This statement is merely another way of saying that the character evolves. It is only within local groups that an allele can have low relative fitness and nevertheless be selected.

This much is obvious, but imagine a person operating outside the group-selection tradition who decides to model the character and population structure represented in Figure 1. That person might not think to calculate the relative fitnesses within each local group first and then take the weighted average of groups in order to obtain the global allele-frequency change. Instead, he or she might calculate a single fitness for each genotype, averaged over all local groups, and use these figures to compute the global allele-frequency change. There is nothing wrong with this procedure; if we were interested only in determining whether the character evolves, it would provide the same answer as the IGS model. It does not, however, make clear the opposing roles of group and individual selection in the evolution of the character. Indeed, using this methodology, it is easy to conclude that the character evolves by individual selection because it has the highest relative fitness throughout the global population and because evolution within local groups was not monitored. To summarize, sharp disagreement over the roles of group and individual selection can emerge simply from one's choice of a method of analysis.

Although this problem is easy to avoid once it is recognized, it pervades the current literature and is a major impediment to our understanding of how the various concepts truly relate to one another. Only two examples will be presented here. Perhaps the most commonly cited example of group selection is the evolution of avirulence in a myxoma virus that was introduced into Australia to control the European rabbit (38, 51, 53, 94). Lewontin (53) was the first to appreciate its relevance:

> When rabbits from the wild were tested against laboratory strains of virus, it was found that the rabbits had become resistant, as would be expected from simple individual selection. However, when virus recovered from the wild was tested against laboratory rabbits, it was

> discovered that the virus had become less virulent, which cannot be explained by individual selection. The key is that the myxoma virus is spread by mosquitoes, which mechanically transfer a few virus particles to the rabbits they bite . . . Each rabbit is a deme from the standpoint of the virus. When a rabbit dies, the deme becomes extinct since the virus cannot survive in a dead rabbit. Morever, the virus cannot be spread from that deme because mosquitoes do not bite dead rabbits. Thus there is a tremendously high rate of deme extinction, with the result that those demes are left extant that are least virulent. This causes a general trend toward avirulence of the pathogen despite the complete lack of selective advantage of avirulence within demes (53, pp. 14–15).

In contrast, consider Futuyma's (35) description of the same example:

> In many interactions the exploiter cannot evolve to be avirulent; it profits a fox nothing to spare the hare. But if the fitness of an individual parasite or its offspring is lowered by the death of its host, avirulence is advantageous. The myxoma virus, introduced into Australia to control European rabbits, at first caused immense mortality. But within a few years mortality levels were lower, both because the rabbits had evolved resistance and because the virus had evolved to be less lethal. . . . Because the virus is transmitted by mosquitoes that feed only on living rabbits, virulent virus genotypes are less likely to spread than benign genotypes. Avirulence evolves not to assure a stable future supply of hosts, but to benefit individual parasites (35, p. 455).

Alexander & Borgia (1) use the same reasoning to conclude that avirulence evolves by individual selection. Clearly, these authors are comparing the fitness of virulent and avirulent genotypes not within local groups (single hosts), but throughout the global population. They are correct that the avirulent type evolves, but their use of the term individual selection to describe its evolution conflicts with the use of the same term within the group-selection tradition.

My second example is the evolution of biased sex ratios. This subject has played such an important role in the history of group selection and is such a remarkable example of the confusion caused by different methods of analysis that its own history is worth presenting in detail.

In *Adaptation and Natural Selection,* Williams used sex ratio as a critical test of the individual- vs group-selection theories (82, pp. 146–57). Williams reasoned that if group benefit correlates with group size, then group selection should produce a female-biased sex ratio that allows for a faster rate of growth. However, if group benefit is maximized at an intermediate size (perhaps to avoid extinction), then sex ratio should be either male- or female-biased, depending on whether group size is above or below the optimum. In this way, the sex ratio would act as a regulator of group size. Williams argued that if group selection does not occur, then genic (individual) selection would produce a sex ratio of 1:1, in accordance with Fisher's (34) principle (assuming obligate sexuality and equal investment in each son or daughter). After outlining the predictions of the two theories, Williams then turned to the evidence.

> Despite the difficulty of obtaining precise and reliable data, the general answer should be abundantly clear. In all well-studied animals of obligate sexuality . . . a sex ratio of close to one is apparent at most stages of development in most populations. Close conformity with the theory [of Fisher] is certainly the rule, and there is no convincing evidence that sex ratios ever behave as a biotic adaptation [i.e. are biased away from 1:1]. . . . Certainly none of these phenomena gives the appearance of an adaptive adjustment to the needs of populations. I conclude that there is no evidence to support the concept of biotic adaptations (82, pp. 151–52).

To summarize, Williams thought that biased sex ratios do not exist in nature in sexual species with equal investment in each son or daughter, but that the existence of biased sex ratios would have constituted evidence for group selection. He evidently regarded this case as one of his best refutations of group selection, for in concluding his book he states, "I would regard the problem of sex ratio as solved" (82, p. 272).

The evolution of sex ratio in an IGS model has been explored by Colwell (21), Colwell et al (22), and Wilson & Colwell (92). Briefly, two alternative alleles code for a 1:1 and a female-biased sex ratio, respectively. Individuals are randomly distrubuted into local groups of size N, which are allowed to grow for a number of generations (G), after which all individuals reenter the global population as dispersers. Fisher's (34) principle operates, causing the allele for female bias to decline in frequency within each group. Sampling error, however, assures that some groups will be initiated by a greater proportion of female-biasing founders than others, and these will grow at a faster rate, ultimately contributing disproportionately to the global population. As a result, evolution within groups promotes a 1:1 sex ratio, which Williams identified as genic (individual) selection, while the differential productivity of groups favors a female-biased sex ratio, which Williams recognized as group selection. If the model is changed so that group extinction occurs above a certain density, then in principle a male-biased sex ratio can evolve by group selection that keeps the group below the extinction threshold. Surely any objective person who first reads Williams's treatment of sex ratio, and then reads the papers cited above (21, 22, 92), will agree that the definitions of group and individual selection are virtually identical.

Since the publication of Williams's book, abundant evidence for the existence of female-biased sex ratios has accumulated, especially among small arthropods in subdivided habitats (15, 46, 48, 92)—a category that includes more species than all the vertebrates combined. Had the IGS model been published in 1967, along with the data that now exist for female-biased sex ratios, the group-selection controversy would most likely be very different from what it is today. Instead, Hamilton (46) presented the theory and evidence for biased sex ratios, describing the population structure of his model as follows:

> Free-moving females search for isolated food objects, or "hosts." Each host is colonized by a certain number and is eventually exhausted through feeding of the progenies. The subpopulation of adults reared on a host mates randomly within itself; no males successfully mate outside their group. Inseminated females emigrate to take part in population-wide competition to discover new hosts (46, p. 480).

This is clearly an IGS model, and the mathematical equivalence between Hamilton's (46) and Colwell's (21) formulation can be demonstrated (15, 21, 48). Hamilton did not monitor evolution within single groups, however, and only calculated the fitness of genotypes for the global population. He attributed the evolution of biased sex ratios not to group selection but to inbreeding and competition among siblings for mates. This case is a good example of how a method of analysis that lumps opposing levels of selection can correctly predict what evolves, but incorrectly interpret the reasons for it. The important parameter is the differential productivity of groups, which is enhanced by the large sampling error caused by the small initial group size. The small group size also promotes inbreeding and competition among brothers for mates, but these alone do not cause the evolution of biased sex ratios (15, 21, 22).

Nevertheless, when stated in a way that did not invoke the concept of group selection, the model and evidence were warmly accepted by evolutionary biologists, including leading proponents of individual selection (e.g. 2, 25, 58). In a final twist of irony, Bulmer & Taylor (13) published yet another derivation of the same model in a paper entitled "Sex Ratio under the Haystack Model," without ever mentioning that this is Maynard Smith's (56) group-selection model or even using the term group selection. In short, biased sex ratios demonstrate group selection according to Williams (82), they are analyzed today with group-selection models, and yet until recently they have been regarded as a triumph for individual-selection theory!

THE MEANING OF THE TERM GROUP The second major issue that must be resolved concerns the definition of local groups. Traditionally, the "groups" of group selection were thought to last for several to many generations. Wynne-Edwards supposed that they persist until driven extinct by selfish types. Maynard Smith did not specify the exact duration of groups in this model, but he assumed that they last long enough for the selfish type to drive the altruistic type extinct. Nevertheless, group duration per se does not appear in the definitions of individual selection, group selection, or altruism. In Figure 1 for instance, the amount of time or number of generations that elapse between Step A and Step D is irrelevant. As far as the actual equations are concerned, a group is defined purely by its density and allele frequency, from which fitnesses are calculated. Uyenoyama & Feldman (73) provide the most formal definition.

> A group is the smallest collection of individuals within a population defined such that genotypic fitness calculated within each group is not a (frequency-dependent) function of the composition of any other group (73, p. 395).

This definition applies to groups of any duration; it also applies to groups that are behaviorally, rather than spatially, formed. Whether in a group individuals choose to interact only among themselves or are spatially isolated and have no choice has no effect on the equations. Finally, I have compared a population broken up into discrete groups of size N with a continuously distributed population in which each individual interacts only with its N-1 surrounding neighbors (87). In the latter case, each individual still belongs to a group of size N, but each forms the center of its own group. These two cases are equivalent to the demes vs neighborhoods dichotomy in population genetics, and both cases yield identical results in IGS models.

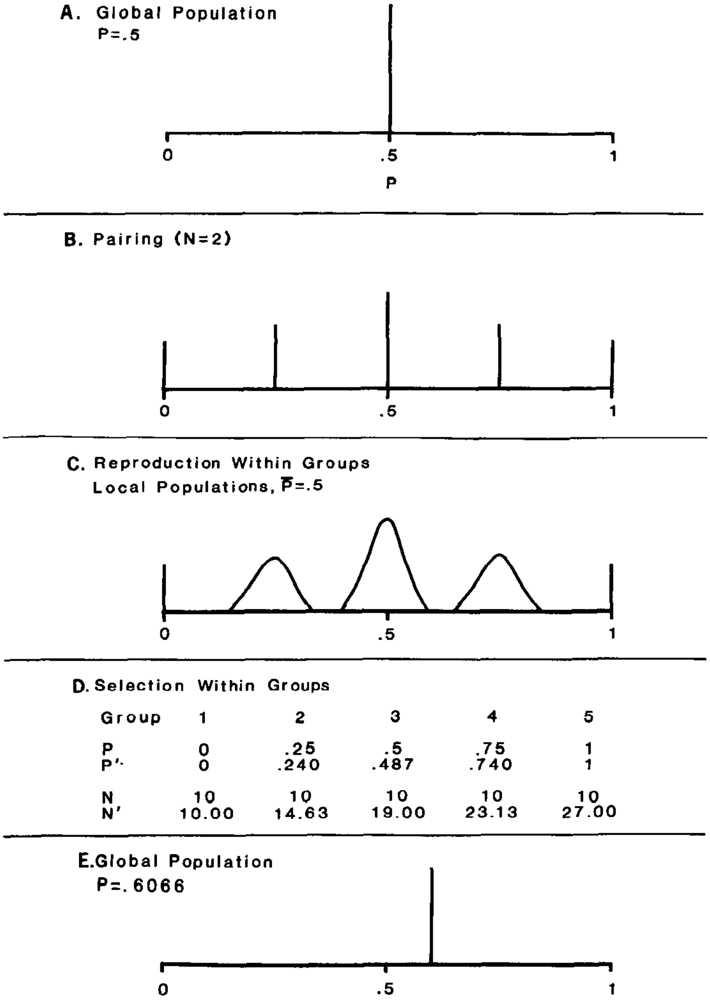
To summarize, even though IGS models fall squarely within the group-selection tradition, the meaning of the term group has been expanded to include short-lived groups, behaviorally formed groups, and "neighborhoods" whose boundaries are not obvious to the human eye. This expansion requires no changes in basic definitions or processes; it follows directly from a notion of groups whose duration is externally imposed, without Maynard Smith's (56) simplifying assumption that between dispersal episodes evolution within each group proceeds to fixation. Indeed, I have stressed that if one adheres strictly to the mathematical definition of groups, then the groups must be very small and defined separately for each trait (the trait group; 85, 87, 90).

The expanded concept of groups led to an important discovery. Many evolutionary models—e.g. kin selection, reciprocal altruism, game theory—consider a single population of individuals that interact in a specified way. This population, however, is not a local group as defined by Uyenoyama & Feldman. For example, with behaviors that are expressed only among siblings, an individual's fitness depends on the genetic composition of its own sibgroup, and is independent of all other sibgroups. For reciprocity models, an individual selects a highly biased subset of other individuals with whom to interact. Fitness depends on the genetic composition of this group, and not on the population at large.

The single population of many evolutionary models must therefore be recognized as a *global* population, containing smaller groups that do conform to Uyenoyama & Feldman's definition. Then it can be shown that these models are not alternatives to group selection, but rather IGS models themselves, in which the opposing levels of selection have not been made clear.

An example of sibling interactions that facilitates comparison with Figure 1 is shown in Figure 2. As before, we start with a global population with the altruistic allele at a frequency of $p = 0.5$. Local groups are initiated by a single fertilized female, as in Maynard Smith's haystack model. This process yields five separate starting frequencies for local groups, as shown in Figure 2, Step B. The relative proportion of these group types will depend on the value of p, assortative mating, and inbreeding.

Each female has a clutch of N offspring, which interact solely among



Group	1	2	3	4	5
P	0	.25	.5	.75	1
P'	0	.240	.487	.740	1
N	10	10	10	10	10
N'	10.00	14.63	19.00	23.13	27.00

Figure 2 IGS model with kin groups. A. Global population, as in Figure 1; B. Formation of groups with one male and one female; C. Formation of sibling groups from the gamete pool of single mated pairs; D. Selection within five representative groups, using Wright's model with $b=2$ and $s=.05$, as in Figure 1; E. The total frequency of A_1 from all groups in Step D.

themselves. These are the groups that conform to Uyenoyama & Feldman's (73) definition. Groups with $p = 1$ and $p = 0$ retain these frequencies in the absence of mutation. Because offspring are drawn from a very large gamete pool, however, local groups initiated at $p = 0.75$, for instance, become distributed with a mean of 0.75 and a variance of $0.5(0.5)/4N$. A polymodal distribution of allele frequencies among local groups is therefore created, as shown in Figure 2, Step C.

Selection now operates within groups, imposing its dual effect; the altruistic allele increases group size but nevertheless declines in frequency within each group. Figure 2, Step D shows selection in five representative groups, with $b = 2$ and $s = 0.05$, as in Figure 1. Notice that the center groups in Figures 1 and 2 both start at $p = 0.5$, and both end with $p' = 0.487$ and $N' = 19$. It is irrelevant that the individuals in Figure 1 are unrelated while those in Figure 2 are siblings. The effect of interactions among siblings on the evolution of altruism occurs not in Step D of Figure 2 but rather in Steps B and C, which create a much greater variation among groups than in Figure 1.

Finally, the offspring reach adulthood and disperse into the global pool. Notice that only a fraction of a generation has been spent within groups. It may be that interactions determining fitness occur within the group, but that the actual production of offspring does not occur until later; this modification does not alter the outcome of the model. Exactly as in Figure 1, the differential contribution of groups causes an increase in the global frequency of altruists, even though evolution within each group had the opposite effect. The final global value of p is greater than in Figure 1, owing to the greater variance in p among local groups.

The generalized version of the model outlined in Figure 2 is actually indistinguishable from Hamilton's inclusive fitness theory, as Hamilton himself was among the first to show (47; for recent reviews see 61, 73). When stated as a group-selection process, however, several interesting features emerge. First, evolution within single sibgroups is no different than for any other kind of groups. The only effect of kin selection is to increase the variance in p among groups. Second, consider a situation in which, after the altruistic characters are expressed, population regulation operates within sibgroups and causes each of them to reach the same density before dispersing into the global pool. In this case the differential productivity of groups is suppressed, while interactions are still exclusively among siblings. The altruistic allele cannot evolve, which demonstrates that group selection, and not kin interactions per se, is the causal factor (12). Finally, the variance in p among groups generated by sibling interactions is actually caused by two rounds of purely random sampling error—the random pairing of mates, followed by a random sampling of their gametic pools.

Hamilton's inclusive fitness theory is basically a different method of analyzing the same process. It correctly predicts the final outcome but does not distinguish clearly between the opposing forces of group and individual selection, as they are defined within the group selection tradition. Instead, Hamilton considered an individual's effect on itself and its neighbors weighted by the probability that the neighbors shared the altruistic allele.

> Despite the principle of "survival of the fittest" the ultimate criterion which determines whether G [an altruistic allele] will spread is not whether the behavior is to the benefit of the

> behaver but whether it is to the benefit of the gene *G*; and this will be the case if the average net result of the behavior is to add to the gene-pool a handful of genes containing *G* in higher concentration than does the gene-pool itself. With altruism this will happen only if the affected individual is a relative of the altruist, therefore having an increased chance of carrying the gene, and if the advantage conferred is large enough compared to the personal disadvantage to offset the regression, or "dilution", of the altruist's genotype in the relative in question (43, pp. 354–55).

It is clear from Figure 2 that every sibgroup containing both alleles actually adds a *lower* concentration of altruists to the gene pool after selection (compare p' with p). Hamilton's statement is correct only when all groups are combined and weighted by their differential productivity.

One consequence of Hamilton's approach is that individual selection becomes defined as "positive absolute effect on self," as opposed to "relative fitness within local groups." Similarly, the term altruism becomes "negative absolute effect on self, positive absolute effect on recipient," in contrast to "declines in frequency within groups, increases the productivity of the group." Much confusion has been generated by the unrecognized differences between these definitions.

The idea that kin selection is a special form of group selection grates harshly on many of those who attribute great importance to the former and none to the latter. A storm of controversy has therefore arisen, in which a few substantive issues are obscured by a cloud of ambiguous terms. Perhaps the most important point to stress is that even when the close relationship is acknowledged, it is easy to rescue the orthodox view. One simply argues that group selection acts as a strong evolutionary force only for those parameter values that are now subsumed under the term kin selection. This approach is actually very close to Williams's own viewpoint. In yet another ironic twist in an already convoluted history, Williams & Williams (84) presented the first comprehensive analysis of sibling interactions in an IGS model that parallels Wright's work (95). As they state: "In the present paper we also use favorable between-group selection to balance unfavorable within-group selection, but our groups are sibships, not mendelian populations" (84, p. 32).

Throughout his book (82), Williams also indicates a continuity between group and kin selection, as E. O. Wilson (94) does as well. Unfortunately, other authors have felt the need to construct a more rigid distinction between kin and group selection. The most common argument is that group selection "requires" spatially discrete groups, whereas kin selection sometimes operates in discrete groups, but does not "need" to do so (1, 14, 24, 57). Because the actual equations define groups as sets of individuals that interact with each other without reference to spatial organization, this distinction is scarcely compelling. Others claim that since IGS models can be translated into the inclusive-fitness framework, they should not be termed group selection (1, 57, 71); the equally close relationship with other group-selection models is not mentioned, however. Other authors criticize the calculation of relative fitness within groups, as if this were an error (1, 14, 24, 49). Still others suggest that differential productivity of groups caused by random variation must be classified as individual selection (14, 24, 41), while variation caused by reproduction within groups must be classified as kin selection (14, 57). I accepted this last suggestion (89) until I realized that every traditional group-selection model begins with groups that are founded by a few individuals that grow into mendelian populations—in which case interactions are largely among kin. Neither reproduction within groups nor interactions among kin can possibly be used to separate kin from group selection. Finally, Maynard Smith's (57) recent suggestion that Wright's model should "fall under the heading of kin selection rather than group selection" (95, p. 278) only emphasizes the futility of trying to separate the two.

The fact that inclusive-fitness models and IGS models are merely different ways of analyzing the same population structure does not mean that one will ever supplant the other. Both have their separate insights and applications. It is imperative, however, always to have the appropriate set of definitions in mind and not to use one set to argue against the other tradition.

IGS models can be applied not only to kin groups, but also to the highly ephemeral groups of unrelated individuals modeled by game theory. Consider, for instance, the standard prisoner's dilemma game (e.g. 5). A global population has two types of individuals—a selfish "hawk" and an altruistic "dove." These types randomly distribute themselves into local groups of size $N = 2$, and fitness is determined entirely within these groups. Doves increase the combined payoff (i.e. productivity) of the group but are selected against in any groups that contain both types. Selection within groups therefore favors hawks, while differential group productivity favors doves. After each round of selection, individuals disperse into the global pool, and the process is reiterated. Without belaboring the point, this example is obviously an IGS model with opposing levels of selection, even though the groups are very different from those that Wynne-Edwards envisioned. As with all IGS models, the altruist can be selected in two ways. First, the variation among groups can be increased, as Fagan (33) shows. This change may happen if doves break off associations with hawks and redraw from the global pool until they encounter a fellow dove; this process is often termed reciprocity (e.g. 10). Second, selection against the altruist within groups can be decreased. The so-called tit-for-tat strategy, for example, involves starting as a dove but converting to a hawk in response to a hawkish opponent (5). Since the hawk always wins the first interaction, the individuals adopting the tit-for-tat strategy are still selected against within every group that they share with a hawk, but at a much slower rate than a dove would be. A tit-for-tat strategy can therefore be selected with only a random variation among groups.

I mention these results not because they are particularly novel (I suspect an

IGS analysis of *n*-person games would be more interesting) but merely to show how easily they fit into a levels-of-selection framework. Some of my colleagues will probably deny that tit-for-tat is an altruistic strategy or that game theory has anything to do with group selection. This is a pity, because in doing so they are rejecting an elegant method of investigating the evolution of socially advantageous traits in all forms of structured populations.

Current Status of Group Selection

I hope I have convinced the reader that the history of group selection has not been a logical and orderly progression of ideas but rather a haphazard and often amusingly convoluted process with many internal contradictions. If I have succeeded, then perhaps the reader will agree with me that the status of the group-selection approach, and its relation to other concepts, needs to be reconsidered. On the one hand, Williams (82) exposed a great deal of silliness in the group-selection tradition. Individuals do not automatically evolve to benefit their fellows; the guiding principle of human evolution is not "one for all and all for one" (3, p. 694); community succession bears no resemblance to individual development (17); and group selection is certainly not "for everything concerning population dynamics, much more important than selection at the individual level (97, p. 20)". On the other hand, the data for sex ratio alone demonstrate that group selection cannot be rejected as uncritically after Williams's book (82) as it was uncritically accepted before it.

I hope I have also convinced the reader that terms have not been defined consistently and that this has caused much confusion. These semantic problems raise a methodological question that is interesting in its own right. What causes scientists to emphasize the unity of ideas at some times and to stress their differences at others? The fact that the population genetics of group selection, sex ratio theory, inclusive fitness, reciprocity, and game theory, are all so similar to one another represents a unification of previously discrepant theories. In a slightly different intellectual climate, this would probably be regarded as a welcome event. So many people think of group selection as a bogeyman, however, that they are reluctant to accept any connection with their own favored ideas, and all efforts go toward finding differences.

As I have already stressed, recognizing the structural similarities among rival theories does not end the controversy. The most important question about group selection remains to be asked: Are socially advantageous characters expressed only among close relatives, or are they more widely distributed in nature? There are two dimensions along which IGS models can depart from sibling interactions. One is by increasing the number of generations spent within the group, such that sibgroups grow into mendelian populations. The other is by increasing the number of individuals that colonize each group, such that unrelated individuals interact with one another from the beginning. I will label as the individualistic view the hypothesis that socially advantageous characters fall off rapidly along both dimensions.

THE DURATION OF GROUPS Consider an IGS model for sibling interactions, such as that represented in Figure 2. Following Hamilton (43–45), assume that altruists increase the fitness of single recipients by an amount *B*, while decreasing their own fitness by an amount *C*. Using the inclusive fitness method, Hamilton showed that the altruistic allele is selected when $B/C>2$. The same result has been obtained with IGS models (e.g. 61, 73).

Now assume that the siblings do not disperse. Instead, groups founded by single fertilized females grow into mendelian populations that persist for a number of generations (*G*) before dispersing into the global pool. Altruists continue to benefit randomly chosen members of their group at their own expense. Can the altruistic allele still evolve? The answer to this question is important, because even though all group members are closely related through a distant ancestor, they would appear totally unrelated to the scientist observing the group several generations after its initiation. Altruism among the group members therefore might not be expected.

Surpisingly, this question has received very little attention, perhaps because Maynard Smith (56) appeared to provide a definitive answer to it. The population structure referred to above is identical to his haystack model, which he constructed to distinguish group selection from kin selection. Maynard Smith did not test the effect of generation time per se, however, but merely assumed that the altruist goes extinct in all groups containing both types. A fairer test would be to follow the consequences of specific fitness functions for both group and individual selection, while varying the number of generations spent within groups. This test has never been done for Hamilton's donor-recipient model, but has been for sex ratio and the "war of attrition" game theory model.

Highly biased sex ratios can evolve even when ten generations are spent within groups between dispersal episodes (13, 15, 92). The biasing allele is continuously selected against within groups, but the differential productivity of groups also increases. Thus, the opposing forces of group and individual selection both intensify, and the equilibrium is only slightly altered. For IGS versions of the war of attrition model, the altruistic alleles are most favored when five to seven generations are spent within the group (D. S. Wilson, unpublished manuscript). In short, there is no compelling reason to believe that group selection can be ignored when several generations are spent within groups. The idea of altruism among distant relatives is intriguing and deserves careful attention.

INITIAL GROUP SIZE The second dimension along which IGS models can depart from pure sibling interactions is by increasing the number of unrelated individuals colonizing each group. The intensity of group selection varies directly with genetic variation among groups. Variation among groups, in turn, declines with the number of unrelated individuals colonizing each group. To appreciate the implications of this, return to Wright's fitness functions (Table 1) and consider a character for which $s = 0$ and $b > 0$. In other words, the character benefits the group but has no effect on relative fitness within groups. This character will always be selected; the rate at which it evolves, however, is inversely related to the initial group size.

Now consider the more interesting situation where $s > 0$ and $b > 0$. This character is favored by group selection (whose intensity declines with group size) and disfavored by individual selection (whose intensity is independent of group size). It follows that a critical initial group size exists, below which the character will evolve, and above which it will not.

Group benefit and individual cost together determine the group size at which a character can evolve. If all socially advantageous traits required extreme self-sacrifice, then they would be restricted to those groups initiated by one or a very few colonists, in accord with the individualistic view. On the other hand, any socially advantageous traits that do not require extreme self-sacrifice should be more widely distributed in nature (36, 87, 90, 91). We therefore arrive at a critical question: What are the trade-offs between group benefit and individual cost? When is a socially desirable character necessarily costly to the individuals possessing it?

This question is so simple and fundamental that one might think it would have been carefully examined. On the contrary, it has been almost universally ignored. In almost all discussions of group selection, group benefit is simply assumed to require extreme self-sacrifice and to be restricted to close relatives as a result. This fact is perhaps the largest irony in the history of group selection and its own development is well worth tracing.

The early proponents of group selection apparently did not recognize individual sacrifice as an important variable. Wynne-Edwards (97), for example, considered reduced personal fecundity, cannibalism, and dominance all as mechanisms to regulate the population, sometimes discussing them even in the same sentence: "Restrictions can be imposed in a number of ways, for instance by each female laying fewer eggs, or eating more of them, or by allowing fewer females to breed" (97, p. 19).

Wynne-Edwards's case was so overstated, and group selection theory was so weak at the time, that Williams (82) invoked Occam's razor to justify rejecting group selection whenever possible. Williams therefore dismissed all behaviors that give the appearance of selfishness (such as dominance and cannibalism) as "not requiring" group selection, and concentrated on providing selfish interpretations for the more problematic examples of reduced fecundity, senility, lemmings running into the sea, and so on.

This procedure may have seemed reasonable at the time, but consider it in the light of Wade's (75, 76) group-selection experiments on *Tribolium* beetles. Wade set up a large number of local groups in the laboratory. After 30 days, reproduction had occurred and the groups' productivity varied. Wade then used these groups to constitute new groups in four separate treatments. In treatment 1, only the smallest groups contributed to the next generation, i.e. groups above a certain threshold "go extinct". In treatment 2 only the largest groups contributed, and in treatment 3 the groups contributed in proportion to their size. Natural selection in these treatments is a combination of group and individual selection. They were compared to a fourth, pure individual selection treatment, in which all groups contribute the same number of individuals, regardless of group size. After eight generations, average group productivity differed in the order treatment 2>treatment 3>treatment 4>treatment 1. Group selection for both high and low group size succeeded in causing a deviation from the individual selection treatment.

Wade's experiments represent an extreme form of group selection that may not be common in nature. Even so, it is interesting to note that the major effect of such extreme group selection was to alter rates of cannibalism (59, 78), which is the very sort of behavior that Williams (82) dismissed as "not requiring" group selection!

No category of behavior as general as cannibalism can be labeled as either selfish or altruistic. Individual selection by itself will produce a specific pattern of cannibalism. Perhaps an individually selected flour beetle eats conspecifics as an optimal forager in order to maximize its own fecundity or perhaps it eats conspecifics to eliminate competition for itself and its offspring. Forces such as these will determine the pattern of cannibalism found in treatment 4 of Wade's experiments. An allele that causes a deviation from this pattern in a way that benefits the group will be selected against within groups as surely as an allele for voluntary birth control. The altered patterns of cannibalism found in treatments 1, 2, and 3 must therefore be labeled altruistic, despite their uncharitable appearance.

There is, however, an important difference between voluntary birth control and altruistic cannibalism—the rate that they are selected against within groups. Voluntary birth control is the ultimate in self-sacrifice and could only evolve in groups founded by one or a very few individuals. By contrast, one can easily imagine a pattern of cannibalism that profoundly affects group size at only a marginal cost to the individual cannibal. This form of population regulation could evolve by group selection even with large initial group sizes, because individual cost is low relative to group benefit. Furthermore, if group size can be regulated either by cannibalism or by voluntary birth control, then the former should evolve even in sibgroups that are capable of evolving the latter (90). Self-sacrifice is always selected against and evolves only when more selfish ways to benefit the group do not exist. Thus, the selfish-appearing behaviors thought "not to require" group selection may be the very behaviors where group selection will be found.

In addition to the simple notion that social benefits need not be individually costly, game theory and quantitative genetics have some potentially remarkable implications that can only be mentioned briefly here. In game theory, fitness often depends on how the majority behaves. Individual selection does not promote a single behavior but rather a large variety of behaviors, depending on the initial composition of each group. Group selection in these models may not oppose individual selection; rather, it may promote a socially advantageous convention that, once established, is also favored by individual selection (D. S. Wilson, unpublished manuscript).

For quantitative genetics, laboratory studies have shown that there is considerable variation among groups, even when the groups are colonized by many unrelated individuals (23, 59, 76–79, 81). This empirical result suggests that the genetics of real populations may be more conducive to group selection than has been indicated by single-locus models. Although the underlying theory still needs to be developed fully, Wade (77) and Craig (23) have suggested that group selection can operate on the nonadditive component of genetic variation that is not subject to individual selection.

To summarize, the distribution of socially advantageous characters in nature depends largely on the trade-off between individual cost and group benefit. This simple point has been ignored until very recently. Instead, any behavior that gives the appearance of selfishness has been assumed to evolve by individual selection, and the search for group selection has been confined to behaviors that give the appearance of charity and good will. This procedure may have seemed reasonable 20 years ago, but today it is no longer appropriate.

Conclusions

Many humans have a strong philosophical bias towards seeing purpose and order above the level of the individual. Others have an equally strong bias towards ascribing selfish motives to all behaviors. Not surprisingly, both of these dispositions are represented in evolutionary thinking and both have been stated axiomatically. The process of converting them into legitimate scientific hypotheses about evolution has not been smooth. The strongly individualistic view that has dominated evolutionary thinking for 20 years certainly is superior to the naive group selectionism that it replaced. It is not, however, the last word on the subject.

Early population genetics models focused on the dynamics of single uniform populations. Against this background, the evolution of socially advantageous characters was difficult to explain. Modern population genetics models incorporate the biological reality of spatial and behavioral heterogeneity. Against such a background, the evolution of socially advantageous characters appears quite plausible. When faced with the difficult task of determining a character's function (if any), benefits to the group cannot be categorically excluded. The prevalence of such adaptations in nature remains to be seen because, despite the blast of words, group selection remains a largely unexplored concept whose important variables have only recently been identified and whose predictions are only beginning to be tested rigorously.

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