SHIFTING THE NATURAL SELECTION METAPHOR TO THE GROUP LEVEL

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ABSTRACT: Group selection is said to occur when the traits of groups that systematically out-reproduce competing groups eventually come to characterize the species. Evolutionists have long disputed over the degree to which group selection is effective—that is, over the degree to which social group characteristics can be attributed to selection on these characteristics. The intractability of this controversy arises from three ambiguities in the natural selection metaphor that manifest themselves when that metaphor is shifted to the group level: (1) uncertainty about what constitutes the analogue for "flock" in the group level metaphor; (2) uncertainty about how to identify the group "parents" of offspring groups; and (3) uncertainty about what constitutes a group trait for the purposes of group selection. When group selection is specified as a theory about the evolution of emergent properties of groups through differential group productivity mediated by quantitative inheritance of group traits, these ambiguities disappear.

Individual selection is said to occur when the heritable traits of individuals that out-reproduce their competitors eventually come to characterize the species. Individual selection would always seem to be the natural explanation for selfish traits of humans—traits like sexual aggressiveness or food hoarding that advance the individual's interests against those of the individual's group. It would seem to oppose the evolution of any altruistic trait—that is, any trait of individuals that systematically favor their competitors. In particular, it would seem to oppose the evolution of altruism directed toward groups—that is, any trait, costly to an individual, that favors the group of which the individual is part. Most evolutionary psychologists are committed to using individual selection to account for the

evolution of human behavior (Barkow, Cosmides, & Tooby, 1992), yet much human behavior appears to be altruistic, both toward other individuals and toward groups. In resolving the contradiction between individual selection and apparent altruism in humans, evolutionary psychologists have generally allowed only two extensions of the natural selection idea, kin selection and reciprocal altruism.

Group selection is said to occur when the traits of groups that systematically out-reproduce competing groups eventually come to characterize the species. Group selection would seem to be a natural explanation for apparently altruistic traits in humans—traits such as group defensive behaviors that appear to advance the group's interests over those of the individual bearing the trait. However, most evolutionary psychologists have avoided group selection explanations. The most commonly given reason is that group selection explanations are implausible— groups can only "reproduce" through the production of individuals, and any costly behavior of individuals that benefited groups would eventually be eliminated from the general population by virtue of the fact that it would be eliminated from every group of which the population was composed. This conclusion is not self-evident. Wilson and Sober have amply demonstrated that no mathematical necessity connects the fate of a trait within local groups of a population to the fate of a trait in the global population (Sober & Wilson, 1998; Wilson, 1980; Wilson & Sober, 1994, 1999).

Counter-intuitive though it may seem, a trait can be negatively selected in each and every local group of a global population and yet be positively selected in the population overall. All that is required for group selection to succeed is:

1) That local groups differ substantially in the proportion of the globally selected trait,
2) That the local groups be ephemeral,[1] and
3) That productivity of each local group be a *positive* function of the proportion of its individuals that bear the globally selected trait.

When these conditions are met, Wilson (1980) argues, group selection of the type called "trait-group" selection can occur. Wilson and Sober (Sober & Wilson, 1998; Wilson & Sober, 1994) and others (See articles in Wilson, 1997; also Michod, 1999) have developed this insight into an argument for multilevel selection as an explanation for group-altruistic behavior in humans and other animals. Further, they suggest that the essential elements of a natural selection argument can explain entities at any level of organization.

The implications of their suggestion are important for the discipline of psychology. As David Buss writes,

> If multi[level] selection theory has any merit, it will have profound implications
> for evolutionary social psychology in pointing to group-level adaptations that
> may have been entirely missed by those focusing on adaptations at the level of
> the individual organism. (Buss, 1999, p. 388)

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[1] Even this condition may not be necessary (see Aviles, 1993; Goodnight, 1993).

Features of human groupings that have up until now been treated as arising from competition among individuals would be interpretable as being caused by competition among groups. Such features need not be limited exclusively (or even primarily) to helping and sharing, but may include such forms of human savagery as gang warfare and genocide. The suggestion has provoked a vigorous debate (e.g., Hartung, 1995, 1996; Thompson, 1998, 1999), which has been marked by some confusion.

One possible source of such confusion is that natural selection is a metaphor whose extension to the group level leads to ambiguities in its interpretation. This paper will identify three such ambiguities, provide resolutions for each, and suggest how their resolution might end the controversy over group selection theories. But before embarking on this project, the essay has some foundation to lay. Many readers may doubt that rigor in the application of scientific metaphors makes any difference or that metaphors have any role to play in science or even that natural selection is a metaphor.

The Use and Abuse of Metaphors

The assertion that Darwin's theory is a metaphor implies no disrespect for it as a scientific theory. Metaphors play an indispensable role in science. The content of our explicit theories is far too impoverished to adequately motivate our research (Hesse, 1974; Lakoff & Johnson, 1980). However, to be scientifically useful, a metaphor must be concrete, and the relation between the model and the thing it is a model of must be precisely specified. The reason for this requirement is that every scientific metaphor generates two kinds of implications, indispensable and dispensable (cf., Hesse, 1974). Indispensable implications are those without which the theory would be either false or vacuous. Dispensable implications are those that the theorist can fairly disclaim. A useful scientific metaphor is so thoroughly specified that all of its users are clear about which parts of the metaphor are dispensable and which are indispensable. When a metaphor underlying a theory is vague and ill specified, its value can be seriously misjudged. The theory can be wrongly attacked by critics who mistake its dispensable implications for essential ones or wrongly sheltered by proponents who make the opposite error.

Evolutionary biology provides some object lessons in the dangers of confusing the essential and the dispensable implications of a scientific metaphor. Evolutionary biology in general, and behavioral ecology in particular, have been characterized by the use—and abuse—of many rich and colorful metaphors (Dawkins, 1976; Krebs & Davies, 1994). Take, for instance, the metaphor embedded in the concept, "manipulation" which is so widely used in behavioral ecology. Early in the use of this metaphor, several philosophers (Midgley, 1979; Stove, 1992) criticized Richard Dawkins for the metaphor's implication that creatures like cuckoos were consciously manipulating creatures like reed warblers. Dawkins correctly replied that this criticism was unwarranted because he had explicitly ruled out this implication out as inessential to his metaphor. Cuckoo scheming was a dispensable implication of the metaphor.

But critics were correct to suspect that Dawkins' use of the metaphor was illegitimate (Thompson & Derr, 1995). To manipulate is to operate skillfully [with the hands]. Manipulate thus implies applying variable techniques to a variable situation to produce a common result. In the cuckoo situation, the species is the first level of organization at which the semblance of manipulation appears. The semblance arises from the fact that each subpopulation of the cuckoo species has idiosyncratic adaptations that suit it to exploit the care-giving behaviors of its particular host species (Wickler, 1968). For instance, the egg-laying female orients to the song of the host and lays an egg that is matched to the host's egg. The egg contains a young cuckoo whose gape is matched to the gape of the host's young. For us to view these features of cuckoos as manipulations, we have to look at each cuckoo subpopulation as one of a set of techniques deployed by the cuckoo species to overcome resistance by the set of hosts, each technique (i.e., each cuckoo subpopulation) matched to the defenses offered by the host species against which it is deployed.

In short, we have to view the cuckoo *species* as doing the manipulating through its subpopulations, the very sort of group level conception that Dawkins would abhor (Thompson & Derr, 1995). Thus, Dawkins (and other users of the metaphor) can be correctly criticized for failing to stipulate that manipulation is NOT action by individual cuckoos or by cuckoo genes. Cuckoo genes and individual cuckoos do not meet the definition because their behavior is invariant; neither the individual cuckoo nor its genes applies variable techniques to a variable situation to produce a common result. This criticism cannot be easily answered because if the metaphor of manipulation is adequately specified, then the inconsistency between Dawkins' genic reductionism and the metaphor would have been obvious, and the term "manipulation" would probably not have gained the wide currency that it now enjoys.

A similar vagueness infects the metaphoric use of "selfish" in the expression, "selfish gene." The metaphor was introduced by Dawkins (1976) as an important corrective to the notion that altruistic behavior of individuals necessarily stood in opposition to the principle of natural selection on genes. However, unless the selfish gene metaphor is adequately specified, it invites us to bring to bear our understandings of telic action on a situation where such understandings are misleading (Hayles, 1995). To be selfish, minimally, is to make choices between self-serving and other-serving alternatives. Genes do not *make* choices; they *are* choices. The first level of organization at which the notion of choice might be brought to bear is the genotype because the genotype is the first level at which alternatives are presented for comparison. Nevertheless, the notion of "selfish X" cannot be rehabilitated by setting X = "genotype," because applying the word selfish to the genotype would vitiate Dawkins' radical, reductive program.

If science is to progress, scientists must take great care to specify their metaphors precisely in order so that they may scrupulously distinguish between the indispensable core of the metaphor and its dispensable periphery. Such an examination would seem to be particularly warranted when the metaphor is being extended—as when, for instance, multilevel selection theorists seek to extend the

selection metaphor from relations among individuals to relations among groups. The first step in achieving such clarity is to state a metaphor in as concrete and particular manner as possible.

The Natural Selection Metaphor

When we say that a trait has come about through natural selection, we are claiming that, in some sense, the trait exists for reasons analogous to the reason for the existence of decorative feathers in a flock of captive pigeons—someone or something arranged the world so that trait-bearers had more offspring than non-trait-bearers (Depew & Weber, 1997). In the metaphor, the production of a flock composed of pigeons with a particular trait—say, with remarkable homing abilities, dramatic flight patterns, or elegant feathers—is taken as the model for the production of a population of better-designed organism such as a sharper-clawed leopard. In the pigeon case, the pigeons in a fancier's loft now have elegant plumage (for example), because in the history of that flock, more elegant pigeons were permitted (by the fancier) to have more offspring, and these offspring themselves were more elegant, with the result that the proportion of elegant pigeons increased in the fancier's flock relative to their alternatives. Similarly, leopards now are sharp-clawed because in the history of the species, sharper-clawed leopards were permitted (by nature) to have more offspring, and these offspring have themselves had sharper claws, with the result that the proportion of sharper-clawed leopards has increased in the population relative to their alternatives.

A Specification of the Metaphor

The specification of the metaphor by reference to the breeding of pigeons is historically apt. Darwin was a pigeon breeder (Bowlby, 1991; Darwin, 1859/1999;[2] Desmond & Moore, 1991). Thus specified, the metaphor suggests at least four analogies between events in nature and events in the pigeon coop.

The first analogy is between variation in the pigeon coop and variation in the wild. For the natural selection metaphor to work, individuals must vary in the wild in a manner analogous to the variation within flocks of pigeons or other domestic stock. The variation must be heritable to the extent that variants in one generation must systematically resemble their offspring in the next.[3]

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[2] "Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons. I have kept every breed which I could purchase or obtain, and have been most kindly favored with skins from several quarters of the world. . . . I have associated with several eminent fanciers, and have been to join two of the London Pigeon Clubs" (*Origin*, p. 12).

[3] Notice that this formulation opens the door for the natural selection of habits, since the mechanism of inheritance is not specified. If a habit conveys benefits to its possessor, is transferred primarily from ancestors to descendants, and varies randomly with respect to its use, then it will evolve by natural selection, on my account. What makes a process natural selection is the structure of the process, not its material substrates. Readers who find this view unorthodox may be reassured that it

The second analogy is between the population of the species and the flock in the coop. To an animal breeder, a "flock" or a "herd" is a breeding group that must be actively defended from dilution by escape or contamination by invasion. The model casts the species as a group of creatures that are reproductively isolated from immigration and emigration. To serve as a model for a species, a flock of pigeons must be limited in number. A pigeon coop that had an unlimited supply of space, food, and water would not have served as a good model for natural populations. If a flock is limited, its breeder must constantly cull it. Darwin, following Malthus, imagined that the same process occurred in nature, although, of course, he imagined that it was disease, starvation, and predation that were doing the culling, not an intentional agent. The specification of the metaphor that makes the species analogous to a flock may seem controversial to some readers. In Chapter 1 of the *Origin,* Darwin explicitly sets species equal to the race, by which he means a breed or type of domestic species, such as an English Bull Dog. But the issue of the origin of such domestic breeds was almost as contentious in Darwin's time as the origin of natural species. In fact, Darwin reports a vigorous debate, which closely paralleled the debate over the modification of species, as to whether the various breeds of a domestic animal were all variants from a single original domestication or descendants from different original species, each closely resembling the contemporary breed. Because of this uncertainty, in the interest of generating a clear metaphor, I have settled on the narrower but less ambiguous "flock." This decision will be reexamined later in the essay.

The third analogy is between artificial selection and natural selection. So strong is the grip of the natural selection metaphor on our imaginations that we now refer to what happens in the barnyard as *artificial* selection. But in Darwin's time, the term was "selection," and it referred to the fact that the breeder, when choosing flock members to be raised and bred, culled out less desirable members. Whether culled animals were killed or merely prevented from breeding, the result was the same: only the desirable animals' offspring come to be represented among the offspring of the next generation.

The final analogy in the metaphor is between the breeder's eugenic goal and features of good design that natural theologists and Darwinians alike agreed were present in organisms. The pigeons of a flock become elegant over time because the breeder has a eugenic goal, to improve the elegance of his flock. Darwin was providing an account of nature that was an alternative to that provided by the natural theologians of his day. Natural theologians saw design features of organisms, such as the fleetness of deer or the sharpness of the leopard's claws, as the product of the intelligence fabrication by a deity. Darwin took for granted the presence of design in nature and provided an alternative account, a natural reproductive bias in favor of better designed organisms, which of course he called natural selection.

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plays little role in the present argument, habits do not normally vary nor are they transmitted exclusively in the manner that natural selection requires.

Dispensable and Indispensable Features of the Metaphor

The most cursory examination of the natural selection metaphor reveals that it has one very important disanalogy. In nature, nothing stands in for the breeder. The implied existence of a Natural Breeder is a dispensable implication of natural selection theory. No one, least of all Darwin has ever proposed that nature acts like an agent ("Nature") when it "chooses" the fleeter deer or the sharper clawed leopard.

But granting that the implication of a selecting agent is dispensable, what is the indispensable core of the Darwinian metaphor? One crucial feature of the metaphor is the identification of each individual in the flock or population by trait possession and by ancestry. In each generation, each individual must be identified by whether it is the offspring of an individual that possessed the well-designed trait and identified once more by whether it is itself a possessor of that trait. Both forms of identification are required to make possible the statement that evolution has occurred because "in the history of the species, possessors of the better designed trait have tended to have more offspring per individual than their less well designed competitors." In other words, offspring identified as being the offspring of individuals identified as being bearers of the better-designed trait were more numerous than offspring identified as being offspring of bearers of the alternative trait. Both forms of identification are indispensably determinate. We do not identify trait-bearers as individuals that "tend to" bear the trait—they do or they don't; nor do we identify descendants as probable offspring—they are or they aren't. Determinacy of the identification is essential because it gives us at least one way to test the theory by direct observation. The natural selection of a trait cannot be demonstrated unless those individuals identified in each generation as being offspring of individuals that bear the trait are increasing in the population.[4] When identification by descent and by trait are put together with differential reproduction and heredity, a proposition is generated that contains four essential parts. A better-designed individual trait has come to characterize the species because:

1) offspring of individuals (*identification by descent*) . . .
2) that bear the better designed trait (*identification by trait possession*) . . .
3) tended to be more numerous (*differential reproduction*)
4) and also tended to be themselves individuals identifiable as bearing the well-designed trait (*heredity)*.

This proposition is the indispensable core of Darwinian theory. It comprises the elements that must be contained in any precise extension of the theory.

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[4] A subtle disanalogy between natural and artificial selection arises in the role of identification in the two. In artificial selection, the identification of traitbearers by the breeder is part of the causal chain of events that leads to its greater reproduction. Identification plays no such role in natural selection. A leopard with sharp teeth doesn't have to be identified by scientists to be favorably selected in nature. I suppose someone determined to see an analogy here could argue that a sharp-toothed leopard that, through some bizarre set of circumstances, had never had an opportunity to chew with his sharp teeth, might be analogous to a pigeon whose elegance had been overlooked by his breeder. I shall not pursue this line of argument.

Widely-Accepted Extensions of the Darwinian Metaphor

The Darwinian metaphor is commonly extended by evolutionary psychologists (and others) to include two situations that are not anticipated in the simplest versions of the pigeon flock model, reciprocal altruism and kin selection.

Reciprocal Altruism. Reciprocal altruism is particularly well accommodated within this framework because reciprocal altruism is simply an example of a situation—like nest-building in birds or dam-building in beavers—where the organism is selected for making changes in its surroundings that favor its future reproduction. Consider, for instance, the trait of reciprocal feeding that exists in the vampire bats described by Wilkinson (1984). Wilkinson demonstrated that bats preferentially feed bats that have fed them in the past and argued on the basis of several facts about the bats that this behavior would be favored by natural selection. First among these facts is that a vampire bat operates with low margins of safety. Because it is a flying creature, a bat cannot build up large fat reserves and therefore must feed at least every other day. Because its resource—large resting ungulates—is spotty and resists being a food source, an individual bat cannot count on finding a food source every night; but when it does find a food source, it can readily collect more blood than it needs to sustain itself for a night. Thus, evolution of reciprocal feeding in vampire bats has come to characterize the species because:

1) offspring of an individual . . .
2) that is a reciprocal feeder
3) tended to be more numerous in the species (because their parents had more reciprocal feeders around them)
4) and also tended to be themselves individuals identifiable as reciprocal feeders.

Reciprocal altruism is selected because it favors an environment around the reciprocal altruist that is conducive to its survival—an environment of reciprocal feeders.

Kin Selection. Showing that kin selection is an extension of the metaphor is more intricate. Readers familiar with animal breeding practices may have noticed that I made an overly narrow explication of the breeder metaphor when I said above that "the natural selection of a trait cannot be demonstrated unless those individuals identified in each generation as being offspring of individuals that bear the trait are increasing in the population." Strictly speaking, artificial breeding programs *can* go forward even though individuals *not* identified as being offspring of individuals that bear the desired trait are increasing in the population. Every beef farmer knows this fact because if such breeding programs were impossible, then tasty beef could never have been bred for. Why? Because the taste test is a destructive one! In general, this problem arises for the breeding of any trait where the identification procedure precludes reproduction. In that case, breeders know

well enough to use relatives (e.g., brothers) of individuals that bear the trait as their breeding stock.

Therefore, in the artificial selection case, meat quality improves in the beef herd because:

1) offspring of the offspring of an individual that is an ancestor of an individual . . .
2) that is itself identified by having tasty meat
3) tended to be more numerous
4) and also tended to be themselves individuals identifiable as bearing the well-designed trait.

The same problem arises in nature with the explanation of any trait that is self-destructive. Consider, for instance, the evolution of the suicidal stinging behavior of honeybee workers. On an account analogous with that of the "evolution" of well-marbled beef, honeybee suicidal stinging behavior has evolved because

1) offspring of a bee that is the parent of a bee
2) that stung
3) tended to be more numerous
4) and also tended themselves to sting.

Those who are familiar with the recent history of sociobiology will recognize this explanation as equivalent to "kin selection." As this analysis makes clear, the term kin selection is a misnomer, since it implies that selection could ever be of any other kind. Any application of the selection metaphor requires the application of *two* criteria, trait possession and kinship (usually parentage). The kinship criterion—or more precisely—that ancestry/descendancy criterion can be more generally stated in the metaphor as follows:

Evolution of trait X occurred because:

1) D-order descendants of individuals that are A-order ancestors of . . .
2) trait-bearers
3) tended to be more numerous
4) and also tended to be themselves trait-bearers.

Selection that is commonly termed "individual" is a special case of the application of the metaphor in which $D = 1$ and $A = 0$. (A first order descendent is an offspring and a 0-th order ancestor is the individual itself.) The selection for altruism directed toward brothers described in Hamilton's classic (1964) paper is another special case, the one in which $D = 2$ (grandchildren) and $A = 1$. Stated in this form, Hamilton's theory is that altruism among siblings came to characterize the species because the grandchildren of grandparents who had children who were mutually altruistic tended to become more numerous (than the grandchildren of grandparents who didn't) and because these same grandchildren were themselves mutual altruists.

Extending the Metaphor to the Group Level

If shifting the natural selection metaphor to the group level is possible, then substituting the word "group" for the word "individual" in a valid individual-level formulation of Darwin's theory should produce a valid group-level formulation.

A better-designed group trait has evolved because:
1) the offspring-groups of groups. . . .
2) that bore the better-designed trait
3) tended to be more numerous
4) and also tended to be themselves groups that bore the well-designed trait.

As we try to interpret this group-level version of the metaphor, three ambiguities arise: (1) What is the analogue for "flock" in the group shifted metaphor? (2) How are groups to be identified by descent? And (3) how are groups to be identified by "trait-bearing?" Before a group-level theory can be rationally evaluated, the metaphor must be specified to remove these ambiguities.

Ambiguity Arising From the Analogy Between Flocks and Species

When the metaphor of selection is applied at the individual level, the "flock" stands in for the species, and the pigeon-to-flock relation in the artificial selection situation is taken as the model for the individual-to-species relation in the natural domain, thus:

pigeon : flock :: individual : species.

The most straight-forward way to apply the metaphor at the group level would be to substitute "group" for individual, which gets us:

pigeon : flock :: group : species.

However, this formulation is problematic. Further substitution gives us:

individual : species :: group : species,

and this result is incoherent. The group-to-species relation is, after all, a component of the individual-to-species relation, the other component being the individual-to-group relation. Where does the individual-to-group relation fit in?

The answer offered by contemporary group selectionists (e.g., Wilson & Sober, 1994) is to decompose the individual-to-species relation into its two components, the individual-to-group relation and the group-to-species relation and to propose that the same relation exist in both, thus:

individual : group :: group : species.

According to our specification of the model, the pigeon-to-flock relation in the artificial domain serves as a model for both the individual-to-group relation and the group-to-species relation, yielding:

pigeon : flock :: individual : group
and
pigeon : flock :: group : species.

Further substitution now yields:

individual : group :: group : species,

which *is* coherent.

This respecified version of the Darwinian metaphor fosters two claims. The first is the individual selection claim. It is that a well designed individual trait may come to characterize the individuals of a social group in the same way that a trait favored by the pigeon fancier may come to characterize the pigeons of that fancier's flock. The second claim is the group selection claim. It is that a well-designed group trait may come to characterize the social groups of a species in the same way that the traits of individual pigeons come to characterize the pigeons of that fancier's flock. This way of understanding the analogue for flock in an extension of the natural selection metaphor to the group level provides an unambiguous specification of the metaphor.

Ambiguity Arising From Identifying Groups by Descent

When the selection metaphor is shifted to the group level, ambiguities arise in how to identify groups by descent. Since we know that the traits of desirable pigeons come to characterize the flock by desirable flock members bearing more offspring than their alternatives, the metaphor must be interpreted in such a way as to specify how "desirable" groups "bear" offspring. In nature, groups "give birth" in two ways, by division and by seeding. A group reproduces by *division* when it segregates into two or more discrete subgroups. Offspring groups remain coherent and their members remain isolated from the offspring groups of other parent groups. A group reproduces by *seeding* when it sends out individuals who join up with other individuals to form new groups. The same group can reproduce both by seeding and by division. Beehives, for instance, reproduce by division when they swarm and by seeding when they send out drones.

How do we identify unambiguously the parents of seeded groups? To get a sense of the problem, imagine a population that consists of ten groups of ten individuals each. The groups disband periodically, mix within a global population, and then reform into new groups of ten at random. Under these circumstances, how should we identify the new groups as descendants of the old? Are all groups that contain at least one "seed" from group one descendants of group one? If such a group also has seeds from groups two and three, is it also a descendant of group two and three? If it contains two seeds from group one and one from group two is it "more of a descendent of group one"? Such a procedure would make descent a quantitative, rather than a qualitative dimension.

Sober and Wilson (1998) are well aware of this problem and embrace quantitative identification of descent as a solution. Groups are identified as parents and offspring of other groups in proportion to the number of elements that the parent passes to the offspring. Quantitative identification of descent alters the group level extension of the theory as follows:

a better-designed group trait has evolved because:
1) groups more seeded by groups . . .
2) that they themselves bear the better-designed trait
3) tended to be more numerous
4) and also tended to bear the well-designed trait.

One advantage of quantitative identification is that it makes unnecessary the distinction between descent by seeding and descent by division. Division can simply be seen as the limiting case of quantitative ancestry in which all the individuals that form an offspring group come from a single parent group.

Quantitative identification of ancestry immediately provides a procedure for determining unambiguously the degree that an offspring group has been seeded by treat-bearing and non-trait-bearing groups. The general idea is that, at any level of organization, we can calculate the "degree of parentage" between an offspring-entity and its parent by knowing the proportion of elements from the next lower level of organization that offspring received from that parent.

Ambiguity Arising From Identifying Groups by Trait

When the selection metaphor is shifted to the group level, ambiguities also arise in how to identify groups by trait. As with identification by descent, groups can also be identified as trait-bearers in two ways, as aggregates and emergents. Aggregate traits are simple summations of the traits of group members whereas emergent traits are traits of groups idiosyncratically. The weight of a rowing team is an aggregate property of the weights of its members because assessing the weight of a rowing team by weighing the individuals will always give the same result as assessing the team's weight by weighing the entire team. The coordination of a rowing team is an emergent property of the team because group coordination is not the sort of property that can be displayed by the individual team members, nor is it a simple sum of their properties—adding up the coordination of each of the teams members would not give the same result as directly assessing the coordination of the team. For instance, group coordination might be a property favored by just the right balance of personality types within the boat. Both aggregate and emergent properties have played a role in the discussion of group selection. The number of altruists in a group is an aggregate property of a group. Functional organization of a group is an emergent property.

Most contemporary group selection theories are aggregate theories in the sense that they seek to explain the constituency of groups, not their properties. Even Wilson and Sober, who invoke the functional organization of groups as an important concept (Sober & Wilson, 1998; Wilson & Sober, 1994), still focus on the explanation of aggregate properties of groups. At the explanatory core of multilevel selection theory is Wilson's trait-group selection idea. Trait-group selection theories characteristically seek to explain an aggregate property of groups, the predominance of group-advantageous, and individually-disadvantageous traits among the group's members. Thus, by themselves, trait group theories of individual altruism do not constitute complete emergent/seeding group selection theories because, although the trait-group selection mechanism is highly compatible with identification by seeding, the feature of the group these models explain—number of altruists in the group—is an aggregate, not a emergent feature of groups.

Intuition tells me that this feature of contemporary group selection theories—that they are aggregate theories—counts seriously against them. Groups only become an interesting puzzle from the point of view of evolution if they have features or characteristics that are unique to them, that is, emergent features. If group selection theory has nothing to say about the problem of emergence, then no wonder it has had such a hard time getting a hearing among readers concerned with the evolution of human groups.

Three lines of argument support this intuition. The first line of argument precedes from the notion that a group selection theory that takes as its explanatory target the number of altruists is an example of a "degenerate" theory . . . that is, a theory that has lost some crucial feature (Thompson, 1993). The missing feature is the concept of design. One of the great ironies of the past 42 years is that despite the fact that George Williams' (1966) classic contains a passionate plea for the study of natural design (as distinct from natural selection), the practical effect of its publication has been to focus attention primarily on natural selection as an explanatory mechanism. Without a systematic study of natural design, natural selection theory has been largely deprived of a systematic phenomenon to explain. Without the anchorage provided by such a systematic description of the explanandum, a theory can easily degenerate into a series of *ad hoc* explanations. In this degenerate form, natural selection theory accounts for no systematic property of organisms but explains only particular characteristics of particular organisms, case by case.

The contemporary group selection literature continues this degenerate sociobiological tradition by failing to focus in a precise way on the problem of what group-level properties it seeks to explain and how these group-level properties get transmitted from ancestor-group to descendant-group. Instead, it has focussed narrowly on the question of how natural selection (understood as positive individual fitness) might accumulate altruism (understood as negative individual fitness). Thus, to the question, Can the features of groups, as such, determine their frequency in future generations? the only answer it gives is in terms of the power of groups to resist individual selection. In other words, aggregate group selection theory is being brought to bear to explain something about the limits of individual selection, not something about groups of organisms per se. A genuine group selection theory must explain the origins of some uniquely group level design feature, that is, an *emergent* trait.

A second reason to limit group selection explanations to emergent groups is that an aggregation of altruists that displayed no emergent properties could never be favorably selected. Imagine two aggregates in competition, an aggregation of selfish individuals and an aggregation of altruists whose altruism has no emergent consequences for the aggregate. The conditions for the altruist group to have more offspring groups than the selfish group requires that something about their altruistic interaction generates a group property favorable to the group, such as good coordination, efficient foraging, skillful defense, or concerted attack. Being nice to one another does not by itself make an aggregate of nice organisms

effective. In short, selection can never be *of* altruists unless it is *for* some group property that the altruists collectively generate (Sober, 1984).

The third reason to focus on emergent group selection theories flows from the properties of the trait-group selection mechanism. The altruist in a trait-group selection model incurs a single unit of cost but gives a unit of benefit for each member of its group. If the trait to which the individual is contributing is an aggregate trait, this feature of the model appears to require each altruist to be a virtual magic pudding of beneficence. Any individual who could meet these conditions would be like a blood donor whose power to donate was determined solely by the number of people around who needed blood. However, if altruism involves contributing to an emergent property of a group, then the requirement that the benefits of altruism extend to all members of the group seems more plausible. Such an altruist would be like a businessperson who offers her warehouse as a place to hold a blood drive. Her costs would remain flat, but her effect would increase with community size over a broad range of size values.[5]

From these considerations, I conclude that the term "group selection theory" should be limited to theories that explain emergent properties of groups.

Recommended Specification of Group Selection Metaphor

When the ambiguities are resolved in the manner recommended, the group selection theory becomes:

A better-designed emergent group trait has come to characterize the species because:
1) groups more descended from groups . . .
2) that bear the better-designed trait
3) tended to be more numerous
4) and also tended to bear the better-designed group trait.

This theory explains the emergence of group traits by reference to a metaphor with the selection of individual traits by a breeder maintaining a flock, the group trait being seen as analogous to the individual trait and the species being seen as analogous to the flock.

Some Stubborn Difficulties

Before this specification of group selection can be offered for evaluation, it needs to be defended from two lines of critique. The first is from individual

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[5] Some readers may worry that this solution to the "magic pudding" problem seems to contradict another constraint of trait-group selection: group fitness must be a function of the number of altruists in the group. How can group fitness be a function of the number of altruists in the group when one altruist is sufficient to serve an unlimited group size? The worry is ill-founded. It is based on the assumption that adding altruists that serve has effects in the same dimension as adding group members that are served and this assumption is gratuitous. A single donation of space for a blood drive for a single month could be sufficient for any reasonable number of participants in that month, and yet it could be still the case that additional space donations (for other months) would greatly increase the effectiveness of the blood drive.

selection proponents, who will assert this formulation of group selection is actually a form of individual selection. The second is from multilevel selection theorists, who will assert that this formulation of group selection excludes the only mechanism of group selection that has been shown to work.

Is This Formulation of Group Selection "Just" a Form of Individual Selection?

To some, the specification of the group selection metaphor proposed above may seem to be uninteresting because it is "just" a case of kin selection, which they in turn think of as a form of individual selection. This objection can be anticipated because kin selection has always been the principal means by which proponents of individual selection have accounted for phenomena that would see to demand group selection explanations. On the surface, this objection would seem to be absurd because, as was pointed out above, kinship is part of identification by ancestry/descent, not part of identification by trait, and, in any case, kinship, being a relation between individuals, cannot by itself serve as a criterion for selecting individuals.

Nevertheless, "kin-selectionists" might lodge a more troubling objection. They might stipulate that kinship is a supra-individual trait, that selection in this case is not "for" kinship but "for" group traits (Sober, 1984), and that group selection is therefore distinct from kin selection only in some strained philosophical sense. Still, they might assert that the two are in practice indistinguishable because group selection works only when the groups selected are composed of kin.

How seriously to take this objection would seem to turn on the answers to two questions: (1) Must group-selected groups be composed of relatives? and, (2) is the selection of relative-groups reducible to selection on the individuals who were the ancestors of the individuals that formed the groups? If the answer to both questions is "Yes" then group selection, the argument runs, is "just" a form of kin selection.

Must group-selected groups be composed of relatives? The assertion that group-selected groups must always be composed of relatives is based on the first analogy in the metaphor, that which relates variation in the pigeon flock to variation in the wild. For any kind of selection to go forward, the items selected must vary in the possession of the selected traits. This feature of the metaphor has always been troublesome because selection tends to reduce variation. Breeders, unlike nature, can always provide more variation by going to market and purchasing "immigrants" from other flocks that suit their fancy. But such seeking out of favorable immigrants is unlike what goes on in nature, where immigration is usually presumed to be independent of trait possession. According to the assertion, selection on groups is unlikely to have sufficient variation available for it to counter the effects of individual selection *unless* groups are composed of relatives. Therefore, for group selection to be effective, it *must* be selection of groups of relatives.

This objection is answered by demonstrations that group selection can be effective in the absence of common ancestry of the members of groups. Although the argument is very technical and beyond my ability to resolve, most participants to the argument (see Maynard Smith & Szathmary, 1995; Michod, 1999) seem to agree that processes other than kin association can produce the necessary variation, but disagree whether those processes are widespread and potent enough to account for any interesting phenomena in nature.

Is the selection of relative-groups reducible to selection on the individuals who were the ancestors of the individuals that formed the groups? All these technical arguments about the answer to question (1) are moot because the answer to question (2) is clearly negative. Even if all cases of group selection did involve kin selection, selection of groups does not reduce to selection upon group-promoting traits in individuals. The reason is that selection acts favorably on kin-group-promoting traits in individuals if (and only if) selection is acting favorably on the groups that these individuals promote. Thus, the relation between group selection and kin selection is exactly the reverse of what proponents of individual selection propose. While it is true, at least sometimes, that group selection can operate in the absence of kin selection, it will never be true that kin selection can operate in the absence of differential productivity of groups (Aviles, 1993; Goodnight, 1993).

Thus, the proposed formulation of group selection theory is certainly logically distinct from individual selection and probably empirically distinct as well.

Does This Formulation of Group Selection Exclude Trait-Group Selection?

I argued above that trait-group selection explanations be excluded consideration as group selection theories because they explain aggregate traits of groups. Given that trait-group selection theories are widely viewed as the most plausible group selection theories, surely they must play some role in a resolution of the group selection controversy. The role proposed for them here is as the mechanism of inheritance that connects selection for group traits in one generation with the occurrence of descendant groups with the same traits in the next generation. One problem for group selection theory has always been to explain how group properties are passed from generation to generation. The answer suggested by trait-group selection theory is that group-promoting traits are passed by the medium of individuals and that the more individuals with "group-promoting traits," the better organized and harmonious is the group, and the more offspring it has. As a genetic system, trait-group selection is the analogue of an individual-level polygenic system in which the fitness of the individual is quantitatively related to the number of alleles of one kind in the set of loci relevant to the trait.

If trait-group selection is to play the role of a "genetic mechanism" in group selection theory, then it must be the case that, for instance, groups with more "group promoting" individuals (an aggregate trait) must be better organized and more harmonious (emergent traits). What sorts of individuals would be group

promoting in this way? What sort of elements which, when aggregated, would foster emergence of some group trait? The answer that comes to mind immediately is "flexible elements." A boat would be a poor competitor if it had all the best coxswains in the race or all the best stroke oarsmen; but a boat with all the most educable rowers in the race might be a very good competitor, since educable rowers could learn the skills appropriate to each position in the boat. Thus, the relationship between emergent traits as a selective force and trait-group selection as an inheritance mechanism may account for why complex organizations in nature seem so often to be composed of generalist elements that become specialized during development to serve different functions within the whole. Think of the body's cells, for instance, which all contain the same genetic information but come to serve very different functions during the course of development. Think of the neurons of the human cortex, which become structured and organized by position and by experience. Think of the workers in a beehive (Seeley, 1995).

Once group selection explanations are examined and specified in the way that this analysis suggests, their potential significance to evolutionary psychology immediately becomes clear. One of the problems of evolutionary psychology has been to explain why humans are such generalists. One explanation for human generality that has been proposed is the unpredictability of the human environment. Unpredictable environments have often thought to select for generalized responses because they prevent adaptations to local or temporary circumstances (Richerson & Boyd, in press).

The analysis of this paper suggests another reason why humans might be generalists—powerful group selection. Selection for aggregate properties at *any* level is impotent to select for functional differentiation. It can, however, select for differentiability. Thus, the undifferentiated brain tissue and generalized behavior potential that characterize human beings and that make human language and culture a possibility may be a direct result of group selection (Boyd & Richerson, 1985; Boehm, 1997). The exact mechanism by which this selection would come about is a combination of group selection, which would assure that functionally integrated groups generate more offspring groups than their nonfunctionally integrated alternatives, and trait-group inheritance, which would assure that aggregations of differentiable individuals are available to form functionally integrated groups.

Conclusion

Ambiguities arising from the shifting of Darwin's metaphor to the group level have troubled the study of social evolution long enough. When the shifted metaphor is specified as a theory about the evolution of emergent properties of groups through differential group productivity mediated by trait-group inheritance, these ambiguities disappear. I hope that an evaluation of the prevalence and power of group selection theory can now proceed on this common ground.

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