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Reviewed work(s):

Source: *The American Naturalist*, Vol. 150, No. S1, Multilevel Selection: A Symposium

Organized by David Sloan Wilson (July 1997), pp. S122-S134

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/286053>

Accessed: 10/09/2012 19:31

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## ALTRUISM AND ORGANISM: DISENTANGLING THE THEMES OF MULTILEVEL SELECTION THEORY

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*Abstract.*—The evolution of groups into adaptive units, similar to single organisms in the coordination of their parts, is one major theme of multilevel selection theory. Another major theme is the evolution of altruistic behaviors that benefit others at the expense of self. These themes are often assumed to be strongly linked, such that altruism is required for group-level adaptation. Multilevel selection theory reveals a more complex relationship between the themes of altruism and organism. Adaptation at every level of the biological hierarchy requires a corresponding process of natural selection, which includes the fundamental ingredients of phenotypic variation, heritability, and fitness consequences. These ingredients can exist for many kinds of groups and do not require the extreme genetic variation among groups that is usually associated with the evolution of altruism. Thus, it is reasonable to expect higher-level units to evolve into adaptive units with respect to specific traits, even when their members are not genealogically related and do not behave in ways that are obviously altruistic. As one example, the concept of a group mind, which has been well documented in the social insects, may be applicable to other species.

Group selection is the process of natural selection operating at the level of groups rather than individuals. Group selection favors traits that increase the fitness of groups relative to other groups. If group selection operates strongly with respect to a given trait, then groups evolve into adaptive units that can be studied in the same way that individuals are usually studied. For example, Lack (1954) used adaptation at the individual level to reason about the evolution of clutch size in birds. He predicted that an intermediate clutch size would evolve to maximize the number of young that successfully fledge. Wynne-Edwards (1962) used adaptation at the group level to reason about the evolution of population size. He predicted that an intermediate density would evolve to maximize the group's survival and contribution to the formation of new groups. The use of adaptation is the same, and it is only the unit (individual vs. group) that is different.

The concept of groups as adaptive units is one major theme of the group selection controversy. Another major theme is the evolution of altruistic behaviors that benefit others at the expense of self. If altruism is expressed unconditionally toward all members of a social group, it decreases the relative fitness of the altruist within the group. However, groups of altruists are more fit than groups of nonaltruists, which can favor the evolution of the trait despite its dis-

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advantage within groups. Darwin (1871, p. 500) clearly grasped the concept of multilevel selection and its relevance to the evolution of altruism over a century ago.

These two themes of the group selection controversy—individuals as altruists and groups as organismic—are often combined, such that an argument against one is treated as an argument against the other. For example, Williams (1971) argued against Wynne-Edwards's theory by imagining a park inhabited by two kinds of robin: one that practiced voluntary birth control to avoid overexploiting its resources and another that maximized its number of fledglings, as predicted by Lack. The prudent type is an altruist compared with the profligate type and has the lowest relative fitness within the population. Williams found it difficult to imagine a process of group selection that could oppose such strong fitness differences within groups and therefore rejected the idea that groups evolve to regulate their population size. The group-level adaptation (population regulation) was assumed to require altruism (voluntary birth control), and both were rejected together.

In the decades that have followed this simple rejection of group selection theory, a more complex relationship has emerged between the two themes of altruism and organism. The purpose of this article is to disentangle the themes and show that many kinds of groups can evolve into adaptive units via mechanisms that do not require strongly altruistic traits. Before proceeding, I want to emphasize that my focus on groups as adaptive units is not intended to diminish the importance of altruistic behaviors per se. Altruistic behaviors do evolve and probably are not as restricted to genealogical relatives as commonly thought (Sober and Wilson 1997; Wilson and Dugatkin 1997). Nevertheless, adaptation is the fundamental outcome of natural selection, so it is appropriate for group-level adaptations to be the central focus of group selection theory. Altruism can be understood only as it relates to group-level adaptations.

#### ADAPTATION AT THE INDIVIDUAL LEVEL

One of the beauties of multilevel selection theory is that the same conceptual framework is applied to all levels of the biological hierarchy. We therefore can begin by considering the well-understood process of selection among individuals within a single population and then frame-shift upward to consider selection among groups in a metapopulation. An individual organism is itself a higher-level unit, a group of genes. Nevertheless, altruism seldom becomes an issue in the study of individual-level adaptations. A gene would be altruistic if it benefited the other genes in the individual at some expense to itself. But, in the standard model of evolution within a single population, a mutant beneficial gene increases the fitness of the entire individual as collective, including itself. Benefiting the higher-level unit (the individual) does not require self-sacrifice on the part of the lower-level unit (the gene) as far as the gene-individual relationship is concerned. For this reason, random genetic variation among individuals is sufficient for individual-level adaptations to evolve. A single mutant allele is present as a heterozygote with a fitness of  $W_{Aa}$ . The wild-type homozygote has a

fitness of  $W_{aa}$ . If  $W_{Aa} > W_{aa}$ , then no more is required for the  $A$  allele to increase from a mutation frequency.

Recent studies of intragenomic conflict have shown that individuals are less stable higher-level units than previously thought (Buss 1987; Maynard Smith and Szathmáry 1995; Michod 1996a, 1997a, 1997b). Genes and other subunits of individuals are increasingly being viewed as social actors in their own right that can potentially increase their fitness at the expense of other subunits within the individual. For example, a meiotic drive gene ( $A$ ) “selfishly” biases its own transmission during gametogenesis, gaining an advantage over the alternative gene ( $a$ ) within heterozygotes (Crow 1979). However, the meiotic drive gene also compromises the fitness of the entire individual, and individuals composed entirely of meiotic drive genes ( $AA$ ) are especially vulnerable to extinction. As Hamilton (1971) and others realized long ago, this would be a standard example of altruism and selfishness for individuals interacting in social groups. The only novelty of the example is that it concerns genes interacting in individuals.

There are two ways that meiotic drive genes and other genes that have a relative fitness advantage within individuals can be eliminated by natural selection. First, the advantages of within-individual selfishness take place only in heterozygotes ( $Aa$ ). If the  $A$  and  $a$  genes are segregated into homozygotes ( $AA$ ,  $aa$ ), as with extreme inbreeding, then the  $A$  allele will go extinct. In general, increasing genetic variation among higher-level units favors altruistic lower-level units. Once again, this conclusion is mundane for individuals interacting in social groups and is novel in this context only because the lower-level units are genes and the higher-level units are individuals.

The second way for genes that have a relative fitness advantage within individuals to be eliminated is for them to be suppressed by other genes, at either the same or different loci. These genes suppress selfishness but are not themselves altruistic. They increase the fitness of the entire individual, including themselves, and therefore require only random genetic variation among individuals to evolve. In this way, a regulatory system is thought to have evolved that largely (although not entirely) eliminates intragenomic conflict and allows individuals to function as the adaptive units we call organisms. It is interesting that intragenomic conflict and its suppression are often described with language that is borrowed from human social interactions—*outlaws*, *sheriffs*, *police*, *parliaments*, *rules of fairness*, and so on (e.g., Leigh 1977; Alexander and Borgia 1978; Alexander 1987).

#### ADAPTATION AT THE GROUP LEVEL

Now that we have reviewed how genes evolve into functionally integrated individuals, we can frame-shift upward to consider individuals in social groups. Imagine that a population of individuals is randomly divided into a large number of groups. A mutant gene appears that causes the individual to behave in a way that benefits everyone in the group, including itself. There are no fitness differences within the group containing the mutant gene, but the entire group contributes more progeny to the global population than do other groups, which causes

the gene to increase in frequency. Every generation, groups will randomly vary in the frequency of the beneficial gene. Groups with the highest frequency will contribute the most progeny to the global population and therefore to the formation of new groups. Ultimately, the beneficial gene will evolve to fixation.

This would be a process of selection among groups in a metapopulation that is identical in every way to the standard model of selection among individuals within a single population. Altruism is not an issue because the gene is selectively neutral within groups. Nevertheless, selection among groups is still required for the gene to evolve. If the population consisted of only one group or many groups that did not vary, the gene would be selectively neutral. A population of groups and genetic variation among groups are required, but random variation is sufficient because the fitness differences among groups that favor the beneficial gene are not opposed by fitness differences within groups. Continuing the example, imagine that all genes were of this sort, benefiting the group at no cost to the individual. Randomly formed groups would then evolve into adaptive units, superorganisms in the same sense that individuals are organisms.

Obviously, this is not the way that group selection is usually portrayed. However, what is wrong with the portrayal? When we examine attempts to answer this question, we discover that they are inconsistent with each other.

Here is one potential answer: Traits that benefit the group at no cost to the individual would indeed evolve easily by group selection. Unfortunately, it is difficult to imagine the existence of such traits. There is no free lunch, and most activities that increase the fitness of entire groups are costly for the individuals that perform them. Group-level adaptations usually require altruism. Williams implicitly used this argument against Wynne-Edwards in his example of robins in the park.

Here is another potential answer: traits that benefit the group at little or no cost to the individual are common in nature, but they have nothing to do with group selection. After all, an individual who performs the activity is increasing its own absolute fitness, so the trait evolves by individual selection. Group selection is required only to explain the evolution of traits that decrease the absolute fitness of the actor (e.g., Dawkins 1979; Grafen 1984; Alexander 1987; Blurton Jones 1987).

These are completely different arguments that are incompatible with each other. The first argument applies the same conceptual framework to all levels of the biological hierarchy but claims that it is costly for individuals to benefit groups, even though it is not costly for genes to benefit individuals. The second argument changes the conceptual framework. A trait that would be considered a higher-level adaptation when the higher-level unit is an individual and the lower-level unit is a gene is considered a lower-level adaptation when the higher-level unit is a group and the lower-level unit is an individual.

The fact that these two arguments against group selection have happily coexisted in the literature is the tip of a much larger iceberg. Group selection became such a heretical concept during the 1960s and 1970s that many evolutionary biologists stopped reading the actual literature. As knowledge of group selection waned, the definitions of major terms such as *individual selection* changed. In

particular, *individual selection* is defined precisely in group selection models as natural selection within groups. If we want to know whether a trait is favored by individual selection, we compare the fitness of individuals that express the trait with the fitness of other individuals in the same group that do not express the trait. Individual selection favors traits that maximize relative fitness within the group. This is not a newfangled definition but dates back to the earliest models (e.g., Haldane 1932; Wright 1945; Williams and Williams 1957; Maynard Smith 1964; Williams 1966; Price 1970, 1972; Hamilton 1975; reviewed in Wilson 1983 and Sober and Wilson 1997).

Outside multilevel selection theory, the term *individual selection* has taken on a much broader range of definitions. Sometimes it is defined as the absolute fitness of the individual, as in the second argument described earlier. Sometimes it is defined as the inclusive fitness of the individual, even though Hamilton (1975) realized many years ago that inclusive fitness theory includes a component of group selection. Sometimes it seems that individual selection is defined as “whatever evolves in my model,” even when the model includes a population of groups with fitness differences within and among groups. There is little rhyme or reason to these definitions, other than a desire to avoid invoking group selection and ignorance of how individual selection is defined within multilevel selection theory.

The desire to avoid invoking group selection has created a widespread double standard in the interpretation of the gene-individual and the individual-group relationships. Virtually all individual-level adaptations evolve in the form of genes that benefit the collective at no cost to themselves. Yet, when individuals benefit their groups at little or no cost to themselves, these traits are not classified as group-level adaptations. Selection among individuals in a single population requires only random genetic variation among individuals, yet group selection is thought to require extreme genetic variation among groups. The social actors that we call genes largely coalesce into adaptive units that we call organisms. Yet the concept of group-level superorganisms is considered heretical, with the possible exception of groups whose members are genetically highly related. This change of perspective that occurs as we frame-shift up the biological hierarchy makes no logical sense and does not exist within multilevel selection theory.

The double standard reaches its peak in the interpretation of rewards, punishments, and other forms of social control that are used to promote prosocial behaviors in humans and probably many other species. As discussed earlier, individual organisms are themselves higher-level units that are vulnerable to subversion from within. The integrity of the organism can be maintained either by extreme inbreeding, which reduces the potential for natural selection within individuals, or by the evolution of genes that suppress intragenomic conflict without themselves being altruistic. Social control, and not inbreeding, is the most important mechanism that allows groups of genes to function as organisms. Frame-shifting upward, we might conclude that social control, not extreme genetic variation among groups, is the most important mechanism that allows groups of individuals to function as adaptive units. It is regrettable that many evolutionary biologists who know little about multilevel selection theory appear

to have reached the opposite conclusion. Extreme genetic variation among groups is treated as the only mechanism for group-level adaptation, and social control is interpreted in a way that seems to deny rather than to explain the existence of groups as adaptive units. Seemingly altruistic behaviors that benefit the group are not really altruistic because they are promoted by rewards and punishments. And the individuals who reward and punish are not altruistic because they benefit (along with everyone else in the group) from promoting the seemingly altruistic behavior. Group-level adaptation appears to collapse into a heap of self-interest (e.g., Alexander 1987).

#### BACK TO BASICS

Clearly, there is a great need for evolutionary biologists to reeducate themselves about multilevel selection theory, which employs the same conceptual framework at all levels of the biological hierarchy. The term *individual selection* has become so ambiguous that it should be avoided or defined clearly and distinguished from other meanings. The terms *within-group selection* and *between-group selection*, which have always been synonyms for *individual selection* and *group selection* in multilevel selection theory, may be preferable because they retain their precise meaning. The mathematics of multilevel selection theory can be challenging (just as the mathematics of inclusive fitness theory can be challenging), but the basic concepts are simple and merely involve comparing fitnesses in the right way. Whenever a population is subdivided into groups, multilevel selection theory treats the single group as an evolutionary unit within which natural selection can occur. Within-group selection promotes traits that maximize the relative fitness of individuals within the group. To discover what these traits are, we must compare the fitness of individuals possessing the traits with the fitness of other individuals in the same group possessing alternative traits. If the traits favored by within-group selection do not correspond to the traits that actually evolve, then something else is required for the model to become predictive. That something may be natural selection operating at a different level of the biological hierarchy, either between genes within individuals or between groups within the metapopulation. In each case, we can employ the same reasoning process, comparing the relative fitness of units within the next higher unit.

When this simple reasoning process is employed, between-group selection immediately becomes a significant and empirically well-documented evolutionary force (see Sober and Wilson 1997 for a general review and Goodnight and Stevens 1997 for a review of laboratory experiments). Groups certainly do not invariably evolve into adaptive units with respect to all traits. However, between-group selection frequently does influence the evolution of traits and does not require extreme genetic variation among groups. Even randomly formed groups can evolve into adaptive units, especially via mechanisms of social control that suppress within-group selfishness without being strongly altruistic. In short, between-group selection must be considered as a serious hypothesis whenever populations are subdivided into groups. Virtually every major subject in

sociobiology needs to be reconsidered in the light of multilevel selection theory, including Wynne-Edward's hypothesis about population regulation. I will now illustrate these general points by focusing on a single subject: the possibility that groups evolve into adaptive cognitive units, or a group mind.

#### COGNITION AS A GROUP-LEVEL ADAPTATION

Group-level adaptations are usually studied in the context of physical activities such as resource utilization, predator defense, and so on. However, groups can also evolve into adaptive units with respect to cognitive activities such as decision making, memory, and learning. As one example, decision making is a process that involves identifying a problem, imagining a number of alternative solutions, evaluating the alternatives, and making the final decision on how to behave. Each of these activities can be performed by an individual as a self-contained cognitive unit but might be performed even better by groups of individuals interacting in a coordinated fashion. At the extreme, groups might become so integrated and the contribution of any single member might become so partial that the group could literally be said to have a mind in a way that individuals do not, just as brains have a mind in a way that neurons do not.

The concept of a group mind may sound like science fiction, but it has been documented in honey bees and other eusocial insects (Seeley 1995, 1997). To function adaptively, a bee colony must make decisions about which flower patches to visit and which to ignore over an area of several square miles; whether to gather nectar, pollen, or water; the allocation of workers to foraging versus colony maintenance; and so on. Seeley and his colleagues have worked out in impressive detail how these decisions are actually made. In one experiment, a colony in which every bee was individually marked was taken deep into a forest where virtually no natural resources were available. The colony was then provided with artificial nectar sources whose quality could be experimentally manipulated. When the quality of one source was lowered below the quality of other sources, workers ceased to visit the inferior source—proof that the colony can perceive changes in its environment and respond adaptively. Yet individual workers visited only one patch and therefore had no frame of comparison. Instead, individuals contributed one link to a chain of events that allowed the comparison to be made at the colony level. Bees returning from the inferior source danced less and themselves were less likely to revisit. With fewer bees returning from the inferior source, bees from better sources were able to unload their nectar faster, which they used as a cue to dance more. Newly recruited bees were therefore directed to the best patches.

The mechanisms of group-level cognition that Seeley documents go beyond the famous symbolic bee dance that allows bees to communicate the location of resources to each other. In fact, many aspects of the group mind are remarkable for their lack of sophistication as far as individual behavior is concerned. The individuals respond to environmental cues and each other in a simple fashion, but the interactions have emergent properties that result in complex and adaptive behaviors at the colony level. For example, the colony acts as if it is hungry



when its honey supplies are low, sending more workers to collect nectar, yet no individual bee is physically hungry. Instead, the state of the colony is communicated by the amount of time that returning foragers must wait to regurgitate their load of nectar to other workers that carry it to empty cells. When resources are scarce and many cells are empty, returning foragers can immediately unload their nectar, which serves as the cue for increasing foraging effort. Even the physical architecture of the colony, such as the location and dimensions of the dance floor, honeycomb, and brood chambers, has been shown to contribute to cognitive function.

It is an important scientific achievement to show that group minds actually exist and are not just fanciful metaphors. However, there is a tendency to think that group minds are restricted to the social insects and other species that are characterized by extreme genetic variation among groups. This returns us to our general theme: if the group mind required extreme altruism, it might well be restricted to the social insects and a few other species. However, the group mind does not require altruism; it requires coordination—individuals interacting with each other in just the right way. If coordination can be accomplished without extreme self-sacrifice, then group minds might be widely distributed in nature.

An example from humans will illustrate the advantages of thinking in groups and how coordination can be achieved without altruism (see Wilson 1997*b* for a more general review). As mentioned earlier, decision making begins with a diversity-encouraging phase, in which possible solutions are imagined, followed by a winnowing phase in which the solutions are evaluated and all but one are ultimately discarded. For many problems, a single individual can imagine only a small subset of possible solutions, and the solutions imagined by different individuals only partially overlap. Thus, groups whose members freely imagine and then pool their potential solutions have an advantage over single individuals or groups that inhibit free thought and the sharing of ideas among their members. It is also possible that free-thinking groups can think of solutions that none of their members would have imagined alone, but this brainstorming effect has been more difficult to demonstrate (Stroebe and Diehl 1994).

Because decision making is a sequential process, the behaviors that are adaptive during one phase become inappropriate during other phases. A study by Kruglanski and Webster (1991) shows how these changes are coordinated in human social groups without altruism becoming an issue. Kruglanski and Webster examined how Israeli scout troops decided between sites for a work camp, a problem not unlike a band of hunter-gatherers deciding where to forage. Individuals had previously filled out a sociometric scale, rating other members of their group for liking, appreciation, and respect. These three measures correlated highly with each other and were averaged to yield a single index of social status. For each group, a member whose score was at the median of the distribution was approached to become a confederate of the experiment and was instructed to advocate a clearly better (conformist) or worse (deviant) site, either early or late in the decision-making process. After the decision was made, members were told that their previous sociometric ratings had been lost and were asked to again fill out the same scale, which enabled Kruglanski and Webster to measure

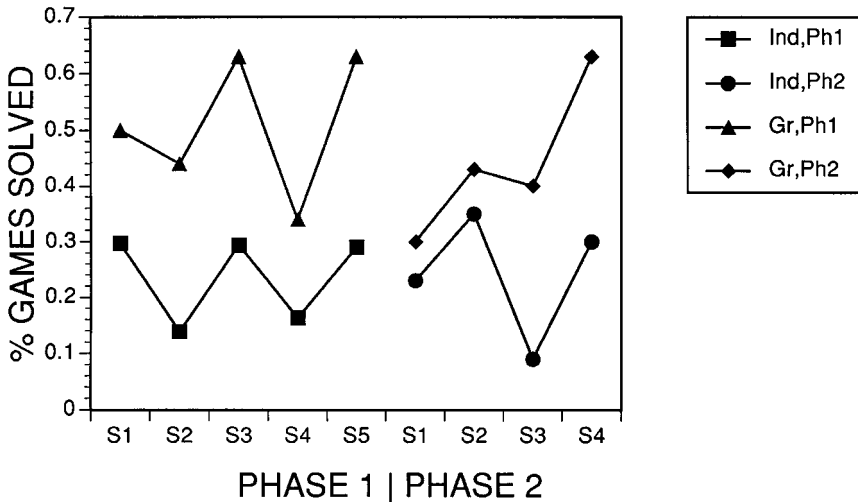


FIG. 1.—The percentage of 20 question games solved by individuals and three-person groups. Phases 1 and 2 consisted of five and four 1-h sessions, respectively. The six groups in phase 1 were split into 18 individuals in phase 2, and vice versa. Groups solved a higher proportion of games than individuals during both phases of the experiment.

changes in social status caused by the decision-making event. The only change in social status was a decrease that occurred when the confederate expressed the deviant position late in the decision-making process. Expressing the same position early in the decision-making process had no effect on status. Thus, not only did social status require participating in a group-level cognitive process, but the social norms surrounding the process were phase dependent, encouraging both diversity and conformity at the appropriate times. Coordination was achieved without self-sacrifice becoming an issue.

The Kruglanski and Webster experiment reveals some of the mechanisms of group-level cognition in humans but does not compare the performances of individuals and groups as decision-making units. Figure 1 makes this comparison for the game of 20 questions, a challenging decision-making exercise in which a word is guessed by asking questions that can be answered with the words *yes*, *no*, or *ambiguous* (J. Timmel and D. S. Wilson, unpublished data). Eighteen individuals and six groups of three individuals played the game for five 1-h sessions. Then the individuals were formed into groups, and the groups were broken into individuals for another 4 h of play. Groups solved almost twice as many games as individuals during both phases of the experiment (ANOVA,  $N = 48$ ,  $F = 19.148$ ,  $df = 1, 44$ ,  $P < .001$ ). Playing the game as a group during phase 1 did not enhance the members' performance when they played as individuals during phase 2. The advantages of thinking in groups require actually being in the group. Figure 2 compares the performance of the 12 groups (ranked from best to worst along the X-axis) with the performance of the average member and the best member playing as individuals. There is no correlation between

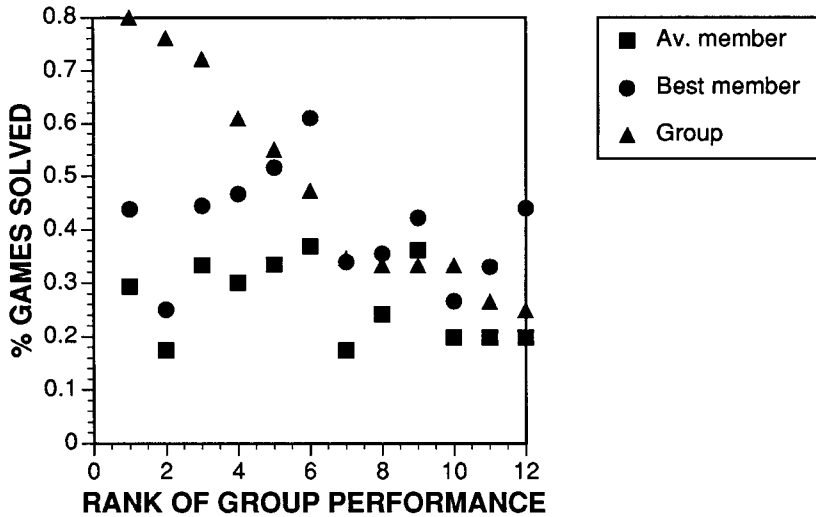


FIG. 2.—The percentage of 20 question games solved by groups (ranked along the X-axis), the average member of the group playing as an individual, and the best member of the group playing as an individual. There is no correlation among these three measures, which demonstrates that group performance is not a simple reflection of individual performance.

group and individual performance ( $N = 12$ ,  $r^2 = 0.020$ ,  $P = .663$ ). Some of the best groups were composed of members who performed poorly as individuals. Thinking as a group requires more than simply allowing the smartest individual to do the thinking.

The group mind was once an accepted concept in the human social sciences. According to Wegner (1986):

Social commentators once found it very useful to analyze the behavior of groups by the same expedient used in analyzing the behavior of individuals. The group, like the person, was assumed to be sentient, to have a form of mental activity that guides action. Rousseau (1767) and Hegel (1807) [1910] were the early architects of this form of analysis, and it became so widely used in the 19th and early 20th centuries that almost every early social theorist we now recognize as a contributor to modern social psychology held a similar view. McDougall, Ross, Durkheim, Wundt, and LeBon, to name just a few, were willing to assume that the group has a mental life that plays a part in the patterning of group behavior. (P. 185)

These early views of the group mind in humans were usually stated in a grandiose form and without attention to mechanisms, similar to naive group selectionism in biology during the same period. They were ultimately rejected by most social scientists in favor of more reductionistic approaches such as behaviorism and methodological individualism (Campbell 1994). Multilevel selection theory suggests that our own species may well be adapted to participate in group-level cognitive processes after all (Boehm 1997; Wilson 1997b). If the group mind does not require extreme self-sacrifice, it can exist in humans as well as in honey bees.

Evidence for group-level cognitive adaptations also exists in other species. The home range of African buffalo herds are a complex mosaic of patches whose quality depends on previous grazing history by the herd, depletion by competing species, regrowth speed, soil fertility, and distance from the current position of the herd. Prins (1996) observed African buffalo for 2 yr before realizing that what appeared to be a mundane stretching behavior was actually a group-level decision-making process.

Some buffalo cows arise, shuffle around a bit and bed down again. At first I interpreted this as “stretching the legs,” but one day I noticed that the cows adopt a particular stance after the shuffling and before lying down again. They seem to gaze in one direction and keep their head higher than the normal resting position but lower than the alert. . . . This standing up, gazing and lying down behaviour continues for about an hour, but the overall impression remains that of a herd totally at rest. Then at about 18.00 hours there is a sudden energizing of the herd. . . . A few moments later, everywhere in the herd buffalo start trekking. The exciting thing is that they start trekking, at the beginning independently of each other, **in the same direction** [Prins’s boldface]. Within seconds, the animals that initiate these movements are followed by other individuals, clusters of movement arise, and within about 3–5 minutes the whole herd of hundreds of individuals moves as if conducted by one master. They totally give the impression that they know where they are going to: apparently, some decision has been taken in the group. (P. 222)

Prins calls this “voting behavior” and has documented its effects on herd movement in impressive detail. Only adult females vote, and females participate regardless of their social status within the herd. When the average direction of gaze is compared with the subsequent movement of the herd, the average deviation is only  $3^\circ$ , which is well within measurement error. On days in which cows differ sharply in their direction of gaze, the herd tends to split and graze in separate patches for the night. In addition to this evidence for communal decision making, there is no evidence for individual leadership. For example, no individual cow or bull stays in the vanguard of the herd for more than a few minutes. Similar forms of voting behavior have been observed (although with less conclusive evidence) in baboon troops (Kummer 1968) and fish schools (Kils 1986; discussed in Pitcher and Parrish 1993).

Prins (1996) regards communal decision making in buffalo herds as similar to the famous bee dance, in which individuals also communicate the direction of resources to each other. Many evolutionary biologists would resist this comparison. The members of bee hives are highly related to each other and reproduce through a single queen, whereas the members of buffalo herds are far less related and compete reproductively. How could both species share an adaptation as “superorganismic” as a group mind? Multilevel selection theory reveals that the comparison may indeed be appropriate. The evolution of group-level adaptations depends not on relatedness per se but on the balance between levels of selection. Groups that must move as a unit are in the same boat with respect to decision making. A good or a bad decision about where to forage will affect all group members (roughly) equally, whereas a group that makes a good decision will fare better than a group that makes a bad decision. If groups whose members interact in a coordinated fashion to gather and integrate information produce better decisions than less coordinated groups, then a group mind will

evolve—by between-group selection. Genetic variation among groups must be sufficient to produce heritable phenotypic variation in the decision-making process among groups, but no more is required.

Multilevel selection theory has developed into a powerful tool for studying adaptations at all levels of the biological hierarchy (see Wilson 1997a for a discussion of selection at the level of multispecies communities). Unfortunately, premature rejection of the theory during the 1960s discouraged many biologists from reading the primary literature and allowed major terms such as *individual selection* to become ambiguous in their meaning. In addition, the evolution of higher-level adaptations has often been confused with the evolution of strongly altruistic behaviors. Returning to the primary literature and disentangling the themes of altruism and organism will enable us to see higher-level adaptations where they exist.

## ACKNOWLEDGMENTS

I thank A. B. Clark, B. Smuts, E. Sober, and the symposium participants for helpful discussion.

## LITERATURE CITED

- Alexander, R. D. 1987. The biology of moral systems. New York: Aldine de Gruyter.
- Alexander, R., and G. Borgia. 1978. Group selection, altruism and the levels of organization of life. *Annual Review of Ecology and Systematics* 9:449–475.
- Blurton Jones, N. 1987. Tolerated theft: suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information* 26:31–54.
- Boehm, C. 1997. Impact of the human egalitarian syndrome on Darwinian selection mechanics. *American Naturalist* 150:S100–S121.
- Buss, L. 1987. The evolution of individuality. Princeton University Press, Princeton, N.J.
- Campbell, D. T. 1994. How individual and face-to-face-group selection undermine firm selection in organizational evolution. Pages 23–38 in J. A. C. Baum and J. V. Singh, eds. *Evolutionary dynamics of organizations*. Oxford University Press, New York.
- Crow, J. F. 1979. Genes that violate Mendel's rules. *Scientific American* 240:104–113.
- Darwin, C. 1871. *The descent of man and selection in relation to sex*. Appleton, New York.
- Dawkins, R. 1979. Twelve misunderstandings of kin selection. *Zeitschrift für Tierpsychologie* 51:184–200.
- Goodnight, C. J., and L. Stevens. 1997. Experimental studies of group selection: what do they tell us about group selection in nature? *American Naturalist* 150:S59–S79.
- Grafen, A. 1984. Natural selection, kin selection and group selection. Pages 62–84 in J. Krebs and N. Davies, eds. *Behavioural ecology: an evolutionary approach*. Blackwell Scientific, Oxford.
- Haldane, J. B. S. 1932. *The causes of evolution*. Longmans Green, London.
- Hamilton, W. D. 1971. Selection of selfish and altruistic behavior in some extreme models. Pages 57–92 in J. F. Eisenberg and W. S. Dillon, eds. *Man and beast: comparative social behavior*. Smithsonian Institution Press, Washington, D.C.
- . 1975. Innate social aptitudes in man: an approach from evolutionary genetics. Pages 133–155 in R. Fox, ed. *Biosocial anthropology*. Malaby, London.
- Hegel, P. T. (1807) 1910. *The phenomenology of mind*. Allen & Unwin, London.
- Kils, U. 1986. *Verhaltenphysiologie Untersuchungen an pelagischen Schwarmen Schwarmbildung als Strategie zur Orientierung in Umwelt-Gradienten Bedeutung der Schwarmbildung in der Aquakultur*. Habilitationsschrift, Institut für Meereskunde. Mathematisch-Naturwissenschaftliche Fakultät, Christian-Albrechts-Universität Kiel, Kiel.

- Kruglanski, A. W., and D. M. Webster. 1991. Group member's reactions to opinion deviates and conformists at varying degrees of proximity to decision deadline and of environmental noise. *Journal of Personality and Social Psychology* 61:212–225.
- Kummer, H. 1968. *Social organization of Hamadryas baboons*. University of Chicago Press, Chicago.
- Lack, D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Leigh, E. G. J. 1977. How does selection reconcile individual advantage with the good of the group? *Proceedings of the National Academy of Sciences of the USA* 74:4542–4546.
- Maynard Smith, J. 1964. Group selection and kin selection. *Nature (London)* 201:1145–1146.
- Maynard Smith, J., and E. Szathmáry. 1995. *The major transitions of life*. W. H. Freeman, New York.
- Michod, R. E. 1996. Cooperation and conflict in the evolution of individuality. II. Mediation of within organism change. *Proceedings of the Royal Society of London B, Biological Sciences* 263: 813–822.
- Michod, R. E. 1997a. Cooperation and conflict in the evolution of individuality. I. Multilevel selection of the organism. *American Naturalist* 149:607–645.
- . 1997b. Evolution of the individual. *American Naturalist* 150:S5–S21.
- Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behaviour in teleosts. Pages 363–439 *in* T. J. Pitcher, ed. *Behaviour of teleost fishes*. Chapman & Hall, London.
- Price, G. R. 1970. Selection and covariance. *Nature (London)* 227:520–521.
- . 1972. Extension of covariance selection mathematics. *Annals of Human Genetics* 35:485–490.
- Prins, H. H. T. 1996. *Ecology and behaviour of the African buffalo*. Chapman & Hall, London.
- Rousseau, J. J. 1767. *A treatise on the social contract*. Beckett & DeHondt, London.
- Seeley, T. D. 1995. *The wisdom of the hive*. Harvard University Press, Cambridge, Mass.
- . 1997. Honey bee colonies are group-level adaptive units. *American Naturalist* 150:S22–S41.
- Sober, E., and D. S. Wilson. 1997. *Unto others: the evolution of altruism*. Harvard University Press, Cambridge, Mass.
- Stroebe, W., and M. Diehl. 1994. Why groups are less effective than their members: on productivity losses in idea-generating groups. *European Review of Social Psychology* 5:271–303.
- Wegner, D. M. 1986. Transactive memory: a contemporary analysis of the group mind. Pages 185–208 *in* B. Mullen and G. R. Goethals, eds. *Theories of group behavior*. Springer, New York.
- Williams, G. C. 1966. *Adaptation and natural selection: a critique of some current evolutionary thought*. Princeton University Press, Princeton, N.J.
- . 1971. Introduction. Pages 1–15 *in* G. C. Williams, ed. *Group selection*. Aldine/Atherton, Chicago.
- Williams, G. C., and D. C. Williams. 1957. Natural selection of individually harmful social adaptations among sibs with special reference to social insects. *Evolution* 11:32–39.
- Wilson, D. S. 1983. The group selection controversy: history and current status. *Annual Review of Ecology and Systematics* 14:159–187.
- . 1997a. The concept of biological communities as functionally organized units. *Ecology* (in press).
- . 1997b. Incorporating group selection into the adaptationist program: a case study involving human decision making. Pages 345–386 *in* J. Simpson and D. Kendrick, eds. *Evolutionary social psychology*. Erlbaum, Mahwah, N.J.
- Wilson, D. S., and L. A. Dugatkin. 1997. Group selection and assortative interactions. *American Naturalist* 149:336–351.
- Wright, S. 1945. Tempo and mode in evolution: a critical review. *Ecology* 26:415–419.
- Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behavior*. Oliver & Boyd, Edinburgh.