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Incorporating Group Selection into the Adaptationist Program: A Case Study Involving Human Decision Making

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This chapter has both a general and a specific purpose. The general purpose is to show how to reason intuitively about natural selection as a multilevel process. The idea that higher-level units such as social groups can be well adapted, in the same sense that individuals are well adapted, has a long history in biology, the human sciences, and everyday thought. For example, the term "body politic" suggests that a human political organization is comparable to a single organism. In biology, group-level adaptations have been regarded as theoretically possible but sufficiently unlikely that they can be ignored for the majority of species in nature (Williams, 1966). Thus, when most evolutionary biologists reason intuitively about natural selection, they think that it is sufficient to ask, "What traits would maximize the fitness of individuals, relative to other individuals in the population?"

More recently, group selection has been reassessed by biologists and may be much more common and important than previously thought (review by Wilson & Sober, 1994; Sober & Wilson, in press). If so, then it is necessary to consider the effects of traits on the relative fitness of groups in addition to their effects on the relative fitness of individuals within groups. Previous discussions of this issue have been rather technical and have not had much impact on the way biologists think intuitively about adaptation and natural selection. It is therefore important to provide an intuitive framework for thinking about multilevel selection.

My specific purpose is to put the framework to use by examining the cognitive processes that allow humans to make adaptive decisions. Throughout their evolutionary history, people have been faced with the challenge of evaluating information from their environment to decide which of many ways to behave. The quality of a decision can have life-or-death consequences, not only for the relative fitness of individuals within a social group, but also for the fitness of entire social groups relative to other social groups. Thus, it is likely that the psychology of decision making has been strongly shaped by natural selection at both the individual and group levels. In addition, psychologists have been interested in decision making for many decades, which has resulted in literally hundreds of empirical studies that can be used as a data base for testing evolutionary hypotheses.

THINKING INTUITIVELY ABOUT MULTILEVEL SELECTION

The individualistic view of adaptation and natural selection has been so influential over the last three decades that it is important to show how it can be fundamentally wrong. Consider the following passage from G. C. Williams (1966):

> Many biologists have implied, and a moderate number have explicitly maintained, that groups of interacting individuals may be adaptively organized in such a way that individual interests are compromised by a functional subordination to group interests.
>
> It is universally conceded by those who have seriously concerned themselves with this problem that such group-related adaptations must be attributed to the natural selection of alternative *groups* of individuals and that the natural selection of alternative alleles within populations will be opposed to this development. I am in entire agreement with the reasoning behind this conclusion. Only by a theory of between-group selection could we achieve a scientific explanation of group-related adaptations. However, I would question one of the premises on which the reasoning is based. Chapters 5 to 8 will be primarily a defence of the thesis that group-related adaptations do not, in fact, exist. (p. 92)

In this passage, Williams makes a theoretical claim that group-level adaptations require a process of natural selection at the group level. He also makes an empirical claim that group-level adaptations do not exist in nature because group selection is too weak. Finally, Williams showed how the evolution of any particular trait can be evaluated with respect to levels of selection. If the genes for the trait spread within a population, then they evolve by individual selection, and the trait is an individual-level adaptation. If the genes for the trait are selectively neutral or disadvantageous within populations, but cause entire populations to survive and reproduce better than other populations, then they evolve by group selection and the trait is a group-level adaptation.

Williams' theoretical claim has withstood the test of time. Group selection remains the only explanation for group-level adaptations, and all group selection models involve the evolution of genes by the differential survival and reproduction of groups. It might seem that Williams' empirical claim has also withstood the test of time, but a closer look reveals that the modern concept of "individual selection" has become very different from Williams' initial conception, as represented by the quoted passage. In particular, so-called theories of individual selection frequently assume that the evolving population is subdivided into a large number of groups but seldom separately examine the relative fitness of individuals within groups and the relative fitness of groups in the metapopulation. Instead, the fitness of each genotype (or gene) is averaged across all groups, which lumps both within- and between-group selection into a single measure of fitness (Wilson, 1989; Wilson & Sober, 1989, 1994; Sober & Wilson, in press). Whatever evolves in the model is said to evolve by "individual selection," and there is no effort to model group selection as an alternative hypothesis. After all, did Williams (1966) and others not show that group selection can be ignored?

Recent group selection models are sometimes referred to as the new group selection, but in many ways they are simply a return to Williams' original conception of group selection as outlined in the passage quoted earlier. When an evolving population is subdivided into a large number of groups, the "new group selectionist" examines the relative fitness of individuals within groups and the relative fitness of groups in the metapopulation. If the trait that evolves is neutral or selectively disadvantageous within groups but increases the relative fitness of groups, it is said to evolve by group selection and to be a group-level adaptation. When relative fitness is carefully partitioned into within- and between-group components, group selection emerges as an important evolutionary force, and many traits turn out to be group-level adaptations, even though the biologists who studied them imagined themselves to be individual selectionists.

Elsewhere, I and others documented the history of specific subjects in detail to show how the concept of individual selection has been stretched to include both within- and between-group selection as understood by Williams (for sex ratio, see Colwell, 1981; Sober & Wilson, in press; Wilson, 1983, for the eusocial insects, see Mitchell, 1993; Seeley, 1989, 1995; for disease virulence see Bull, 1994; Sober & Wilson, in press; for inclusive fitness theory, see Hamilton, 1975; Sober & Wilson, in press; Wilson & Sober, 1989, 1994; for game theory, see Sober & Wilson, in press; Wilson & Sober, 1994; for human social groups, see Sober & Wilson, in press; Wilson & Sober, 1994). For the purposes of this article, I will simply ask the reader to accept two basic points: (a) Group selection can no longer be dismissed as casually as it has been during the past three decades. Evolutionary biologists must seriously consider the possibility of adaptation at more than one level of the biological hierarchy. (b) The new group selection requires a reorganization of familiar theories in a way that shrinks the concept of individual-level adaptation and broadens the concept of group-level adaptation. For example, kin selection and evolutionary game theory are widely regarded as alternatives to group selection that explain altruism and cooperation in individualistic terms. However, both of these theories assume that the evolving population is subdivided into groups: kin groups in the case of inclusive-fitness theory and n-person groups in the case of game theory. When fitnesses are examined within and between these groups, it turns out that altruism and cooperation are always selectively disadvantageous within groups and evolve only by increasing the fitness of groups relative to other groups (Hamilton, 1975; Sober & Wilson, in progress; Williams and Williams, 1957; Wilson, 1983; Wilson and Sober 1989, 1994). These theories are therefore special cases of group selection rather than alternatives to group selection. It is difficult for some evolutionary biologists to make this transition, but there is no alternative if we wish to return to the concepts of within- and between-group selection as developed by Williams (1966).

The reorganization of familiar theories has led some biologists to advocate a form of pluralism in which each framework is equally legitimate (Dugatkin & Reeve, 1994; Holcomb, 1994). Which framework to employ then becomes a matter of taste, and those who prefer what Dugatkin & Reeve call *broad-based individual selection* do not need to change their intuition at all. It would be strange if this were true. After all, the rejection of group selection was treated as a momentous event in evolutionary biology, and for 30 years it has seemed terribly important to avoid thinking about groups as similar to individuals in their functional organization. If it turns out that group selection is important after all, should this not have some impact on the way we think about adaptation and natural selection?

The Adaptationist Program

The centerpiece of evolutionary theory is the concept of adaptation, or a fit between the properties of the organism and the properties of the environment, which evolves by natural selection. Adaptation is a central concept, not only because it is important, but also because it is so easy to employ. It is relatively simple to predict the traits that will maximize fitness in a given environment, at least compared to the task of unravelling the details of phylogeny, genetics, development, and physiology. That is why Darwin was able to achieve his fundamental insights despite his almost total ignorance of phylogeny or the mechanistic processes that make up organisms.

It is important to realize that adaptationist thinking does not deny the importance of other factors such as phylogenetic, genetic ,and developmental constraints. Even if a population is not well adapted to its environment, it is important to know what it would be like if it were, which allows deviations from the optimal phenotype to be interpreted (Orzack & Sober, 1994). Thus, even after we acknowledge that there is more to evolution than natural selection (and more to human nature than evolution), it is still useful to ask this simple question: "What would the population be like if it were adapted to maximize fitness in its environment?"

As previously mentioned, most biologists have been trained to ask this question at the individual level and to avoid asking it at the group level. If group selection is a legitimate possibility, however, we must explicitly ask the question at all relevant levels of the biological hierarchy. I now describe an appropriate procedure as a number of steps, although I do not wish to imply that the steps must be taken in order or that all of them are required for the study of every trait.

Step 1: Ask the question: What Would Groups be Like if Between-Group Selection Were the Only Evolutionary Force?

In this case, groups will be "superorganisms" functionally designed to maximize their survival and reproduction, relative to other groups. For example, if we are interested in predator defense, we might decide that the optimal group organization requires that at least one individual not be feeding and scanning the environment for predators at all times. If we are interested in decision making, we might decide that the optimal group organization will include one phase in which the group members separate to acquire information from different parts of their environment, a second phase in which they pool the information, a third phase in which they assess the information, and so on.

Step 2: Ask the question: What would groups be like if within-group selection were the only evolutionary force?

In this case, individuals will be functionally organized to maximize their survival and reproduction, relative to other individuals within the same group. For example, we might decide that it is adaptive for an individual to issue an alarm call when predators are absent, which distracts other members of the group and allows the individual to feed. If we are interested in decision making, we might decide that it is adaptive for individuals to withhold information or present false information that will increase their relative fitness.

This step of the procedure corresponds to what Williams (1966) understood as within-group selection. However, it is important to distinguish it from the broadened form of individual selection that has developed since Williams (1966). For example, consider a population that is subdivided into a large number of groups and a mutant behavior that increases the fitness of the actor by one unit and the fitness of everyone else in the actor's group by two units. If X is the baseline fitness, then the fitness of the mutant is $X + 1$, and the fitness of the average non-mutant is X because the vast majority of nonmutants exist in groups without the mutant. Many biologists would say that the behavior evolves by individual selection, but this conclusion is based on comparing the fitness of the mutant with the fitness of nonmutants averaged across groups. If we employ Williams' definition of within- and between-group selection we discover that the mutant has the lowest relative fitness within its own group ($X + 1$ vs. $X + 2$) but that groups with the mutant are more fit than groups without the mutant. This is a specific example of the general claim made earlier, that the modern version of individual selection includes both within- and between-group selection as defined by Williams. In any case, it is important to base step 2 of the procedure on a comparison of fitnesses within single groups.

Steps 1 and 2 bracket the possibilities of what can evolve by natural selection. We do not expect populations to lie at either extreme, but we do expect them to be somewhere between. The next step is to determine where a given population is likely to lie between the extremes.

Step 3: Examine the basic ingredients of natural selection at each level of the hierarchy.

The process of natural selection requires three basic ingredients: phenotypic variation among units, heritability, and differences in survival and reproduction that correlate with the phenotypic differences. To determine the balance between levels of selection, we need to examine these ingredients at each level.

Step 3a: Ask the question: What is the potential for phenotypic variation within and among groups?

Consider an asexual population that consists of two phenotypes, A and B, in frequency p and $(1 - p)$ respectively. Imagine that we subdivide the population into groups by allowing each individual to reproduce and form a clonal group of size N. The metapopulation now consists of a fraction p of groups that are pure A and a fraction $(1 - p)$ groups that are pure B. This kind of population structure is maximally conducive to between-group selection because there is no phenotypic (or genetic) variation within groups on which natural selection can act. Now imagine that we compose the groups by placing exactly p A-types and $(1 - p)$ B-types in each group. This kind of population structure is maximally conducive to within-group selection because there is no phenotypic (or genetic) variation between groups on which natural selection can act. Between these two extremes are a great range of population structures in which phenotypic variation is partitioned into a within-group component and a between-group component. For example, if we compose groups of size N by placing individuals randomly into each group, there will be a certain amount of phenotypic (and genetic) variation among groups that is given by the binomial distribution, whose variance is $p(1-p)/N$. The partitioning of phenotypic variation within and among groups obviously has a strong influence on the balance between levels of selection.

Although kin selection theory is often described in terms of the proportion of shared genes that are identical by descent, the coefficient of relationship (r) is better understood as an index of variation within and among groups. This is not a controversial statement and has been accepted by virtually all theoretical biologists, including Hamilton (1975). For example, $r = 1$ represents the clonal population structure described above. Interactions among full siblings, or $r = .5$, represents a population structure in which groups of size N are composed by first picking a male and female at random from the metapopulation and then forming groups of size N from their gametes. The resulting variation among groups is far greater than if we had picked N individuals directly from the metapopulation, but less than the variation that results from asexual clonal reproduction ($r = 1$).

Kin selection theory sometimes makes it seem as if r is the only important factor determining the amount of variation within and among groups. In fact it is only one of many factors, which suggests that group selection can be a potent force even when the genetic relatedness among the interacting individuals is low. I briefly describe three other factors that can create large phenotypic differences among groups.

Complex Genotype–Phenotype Relationships. In a classic experiment, Wade (1976, 1977) created groups of flour beetles by picking $N = 16$ individuals at random from a large laboratory population and placing them in small vials with flour to reproduce. After 37 days he measured the total number of offspring produced by each group, which can be considered a group-level phenotypic trait. The variation among groups was enormous, ranging from 365 progeny for the most productive group to only 118 progeny for the least productive group. This amount of phenotypic variation could never have been predicted from the relatively large number of individuals that initiated each group. In other words, if we assume that group productivity is the sum of individual fecundities, randomly composed groups of $N = 16$ beetles could not possibly vary as much as observed in the experiment. Group-level variation must therefore reflect an interaction among individuals, rather than the additive sum of their properties. In a series of follow-up experiments, Wade (1979) and McCauley and Wade (1980) showed that group productivity depends on a complex interaction between a number of traits including development, cannibalism, and sensitivity to crowding. This example illustrates that the relationship between the genetic composition of a unit and the phenotype of that unit can be complex. Just as a small genetic change can have a large phenotypic effect at the individual level, small genetic differences between groups can lead to large phenotypic differences. This important point is missed by most population genetics models, including kin selection models, which tend to assume an additive relationship between genetic and phenotypic variation.

Assortative Interactions. In kin selection models and many traditional group selection models, high phenotypic (and genetic) variation among groups is created by the process of reproduction. In other words, groups of size N are formed by initiating the groups with a smaller number of individuals, who then reproduce to form groups of size N. The variation among these groups is greater than among groups initiated directly with N individuals.

Another way to create high variation among groups is by assortative interactions. To pick an extreme example, imagine a very large population of individuals who differ in their cooperativeness. Suppose that every individual knows the cooperativeness of every other individual and can freely choose whom to associate with in groups of size N. Every individual will be rejected by more cooperative individuals, and each individual will reject less cooperative individuals, leading to a population structure in which there is no variation within groups and maximal variation among groups. This population structure is as favorable for group selection as clonal reproduction, even though group members are genealogically unrelated to each other. The assumptions of this example are obviously unrealistic, but more realistic assumptions can still lead to highly nonrandom groupings, even if they do not achieve the ideal of eliminating variation within groups (Wilson & Dugatkin, in press). Assortative interactions are likely to be an especially important mechanism for creating phenotypic variation among human groups (Frank, 1988).

Social Norms. So far, I have assumed, along with most theoretical models, a strong form of genetic determinism in which individuals are altruistic (for example) because they have a gene for altruism. Evolutionary biologists are quick to admit that this is just a simplifying assumption and that a complex array of psychological mechanisms separate the phenotype from the genotype in many species. Nevertheless, the simplifying assumption is defended as useful because adaptive psychological mechanisms will prompt the organism to adopt the phenotype that would evolve in a given situation, given enough time and a simple genetic basis. We do not have a single gene for pulling our hand away from fires, but our adaptive psychological mechanisms cause us to behave as if we do.

This defense of genetic determinism as a useful simplifying assumption is warranted to a degree, but it is especially misleading when it comes to thinking about phenotypic variation within and among groups. In particular, human groups are often behaviorally homogenous in ways that could never be predicted from their genetic structure. Homogeneity is achieved, not by the assortative interactions of individuals with fixed phenotypes as outlined earlier, but by social norms that cause phenotypically plastic individuals to converge on a single behavior. The psychological mechanisms that structure social norms and phenotypic plasticity may well be biologically adaptive, but they also radically change the population structure, creating a pattern of phenotypic variation within and among groups that verges on the clonal, even when the groups consist of many thousands or even millions of genetically different individuals (see Boyd & Richerson, 1985, for a more thorough discussion of group selection and cultural evolution).

We may summarize step 3a by saying that phenotypic variation within and among groups can be influenced by many factors. The evolutionary literature sometimes gives the impression that genetic relatedness is the primary factor determining phenotypic variation among groups, leading to the expectation that group-level adaptations should be found only within groups of highly related individuals. This expectation is misleading because extreme phenotypic variation frequently exists among groups of genetically unrelated individuals. By focusing on phenotypic variation as one of the primary ingredients of natural selection, we begin to see new possibilities for group selection that were not forthcoming from kin selection theory.

Step 3b: Ask the Question: Is the Phenotypic Variation Heritable?

The simplest way to approach the issue of heritability is to imagine or actually perform a simple experiment. In a population of units that reproduces and varies phenotypically, divide the phenotypic distribution in half and allow each to reproduce as a separate population. If the phenotypic differences between the populations persist into the next generation, then they are least partially heritable.

The value of this experiment is that it does not attempt to identify the specific mechanisms that are responsible for heritability. The continuity between generations can be caused by genetic factors, cultural factors, or both. From the standpoint of natural selection, the specific mechanism does not matter as long as there is continuity between generations.

At the individual level, every offspring has exactly one (for asexual species) or two (for sexual species) biological parents. For sexual species, each parent contributes roughly the same amount of genetic material, although there are important exceptions (e.g., cytoplasmic genes, which are inherited only from the mother). Genetic inheritance becomes more complicated when we consider nonadditive genetic interactions (epistasis), which can cause offspring to become very different from their parents phenotypically, despite the fact that they share the same genes. When we consider cultural transmission, mechanisms of inheritance at the individual level become even more complex. A single offspring can have many parents who make unequal contributions, and so on. These mechanistic details are important, but they are also still poorly understood after more than a century of research. At the intuitive level we are forced to rely on the raw fact of heritability, much as Darwin did.

Heritability at the group level is even more complex than at the individual level. In some species, new groups are formed by a budding or fissioning process, such that each group has a single parent. In many other species, the members of any given group are derived from more than one group. Complex interactions among individuals in a group can have effects comparable to epistatic genetic interactions within individuals. The possibilities become so complex that we are forced to retreat to the more empirical question of whether phenotypic continuity exists, regardless of the mechanisms responsible for the continuity. For example, it would be almost impossible to know if the variation that Wade observed in his groups of flour beetles is heritable without actually forming new groups from old groups in a variety of ways. The empirical result is that group-level variation is heritable and can be selected, even though the group phenotype is caused by complex interactions among the group members and new groups are derived from multiple parental groups (Wade, 1977; Wade & McCauley 1980).

When we examine the phenotypic continuity of human groups, we find that it is often highly stable. In fact, many phenotypic differences between human groups persist despite extensive mixing of the individuals that make up the groups. This happens because individuals that move from one group to another are often expected to (and do) abandon the social norms of their old group and adopt the norms of their new group. Thus, phenotypic plasticity at the individual level, coupled with certain kinds of social norms, create a degree of heritability at the group level that could never be predicted from the size and mixing among groups. This is another example of how the simplifying assumption of genetic determinism, although useful for some purposes, can be misleading about the fundamental ingredients of phenotypic variation and heritability at the group level.

Step 3c: Ask the Question: What are the Fitness Consequences of Phenotypic Variation Within and Among Groups?

If heritable variation exists, then the differential survival and reproduction of units will cause evolutionary change, resulting in a fit between the properties of the unit and the environment that we call adaptation. The rate of evolutionary change and the degree to which natural selection at a given level prevails against opposing forces depends on the intensity of selection. For example, Wade's (1976, 1977) experiment included two group selection treatments. In the first, each group contributed to the next generation in proportion to its productivity. The second treatment was a form of truncation selection in which the least productive groups were discarded and only the most productive groups contributed to the next generation. Group selection occurred in both treatments but was more effective in the second because the fitness differences between groups were greater.

When a single trait (such as altruism) is selected against within groups but favored at the group level, the outcome will depend on the intensity of selection in addition to the amount of heritable variation at each level. For example, some environments are so harsh that it is difficult for a single individual to survive and reproduce on its own. The advantages of group-level functional organization can be so great in these environments that even behaviors with low relative fitness within groups can evolve. The same traits will not evolve in more benign environments because they do not produce the group-level advantages that compensate for the individual-level costs.

Fitness differences can be imposed, not only by the external environment, but also by social norms. Consider a behavior, *x*, that has a positive effect on the group but a substantial cost to the individual performing the behavior. An example might be sentry behavior, in which the sentry must refrain from eating (individual cost) in order to scan for predators (group benefit). Suppose that the balance between levels of selection is such that we would not expect this behavior to evolve by itself. Now consider a second behavior, *y*, that causes individuals to reward other individuals who perform *x*. For example, a female might be sexually attracted to males who perform sentry duty. Behavior *y* has a positive effect on the group to the extent that it causes others to perform *x*, and involves an individual cost, because rewarding *x* requires at least a small amount of time, effort, and allocation of resources that could have been used otherwise. Behavior *y* is therefore altruistic in the same sense as behavior *x*, but the balance between levels of selection is not necessarily the same. In particular, it is often possible for some individuals to provide very large rewards and punishments to others at trivial cost to themselves. Behaviors *x* and *y* may therefore evolve as a package when behavior *x* cannot evolve by itself (Sober & Wilson, in press). In general, the balance between levels of selection can be significantly altered when rewards and punishments are used to restructure the costs and benefits of other behaviors. These kinds of social controls are often interpreted as advantageous for the individuals who do the rewarding and punishing, but a careful analysis of fitness differences within and among groups shows that they are often group-level adaptations that evolve easily because the group-level benefits greatly outweigh the individual-level costs.

An Example of How the MultiLevel Framework Has Been Used Within Evolutionary Biology

The framework that I have sketched for thinking about multilevel selection is not new and, in fact, was employed by Williams (1966), who had to think carefully about group selection before rejecting it. To make the framework less abstract, I wll briefly show how Williams used it to address an important biological problem, before applying it myself to the subject of human decision making.

Williams' (1966) most convincing test of individual versus group selection involved the evolution of sex ratio. Fisher (1930/1950) had shown that natural selection within groups favors an even sex ratio because all offspring have exactly one father and one mother, so whichever sex is in the minority has the most offspring. Williams reasoned that an even sex ratio is not necessarily optimal from the standpoint of the group. If it is beneficial for the group to produce as many offspring as possible over several generations, it should have a highly female-biased sex ratio. Note that Williams was employing steps 1 and 2 of the procedure outlined earlier, by determining what would evolve by pure within- and between-group selection. Williams was unaware of any examples of female-biased sex ratios in nature, and therefore concluded that there was no evidence for group selection. He was so pleased with his empirical test that in the concluding section of his book he stated: "I would regard the problem of sex ratio as solved" (p. 272).

Williams' analysis of sex ratio shows that the multilevel framework can be useful even if it is not followed to completion. Williams completed only the first two steps of the procedure, but this was sufficient for him to make a prediction that could be tested empirically. In general, steps 1 and 2 of the framework are relatively easy because they involve thinking about adaptive design. Step 3 is more difficult because it involves thinking of the mechanistic details of the natural selection process. If adaptive design at the individual and group levels are sufficiently different from each other, then steps 1 and 2 can furnish testable predictions without one knowing much about step 3. Of course, step 3 is required for a deeper understanding.

One year after the publication of Williams (1966), Hamilton (1967) provided many examples of female-biased sex ratios and a theory to explain them, in which groups are colonized by a certain number of individuals whose offspring mate with each other before the daughters disperse to colonize new groups. Despite the fact that Hamilton's theory requires groups, it was interpreted as an example of individual selection for many years until Colwell (1981) showed that it is a mathematical version of Williams' verbally stated hypothesis, in which female-biased sex ratios have a low relative fitness within groups and evolve only because they increase the productivity of groups relative to other groups. Williams (1992, p. 49) has recently agreed with this interpretation. Hamilton's theory is an important advance over Williams' verbally stated hypothesis because it examines step 3 of the framework outlined earlier, allowing us to determine where any given population is likely to lie between the two extremes determined by steps 1 and 2. For example, if groups are initiated by single females, there is maximum variation among groups and the sex ratio is expected to be highly female biased. Increasing the number of individuals colonizing each group shifts the balance in favor of within-group selection, causing the sex ratio to converge on an even proportion of males and females. Subsequent theoretical models have elaborated on step 3 of the procedure, exploring the effects of local population regulation (Wilson & Colwell, 1981), multiple generations spent within groups (Aviles, 1993), and other factors. In general, the empirical data support the predictions of these more detailed models.

A careful reading of Williams shows that he has consistently employed the multilevel adaptationist program throughout his career, defining individual selection as gene frequency change within single groups. This has led him to interpret kin selection as a form of group selection (Williams & Williams, 1957), and to accept both female-biased sex ratios and the evolution of reduced virulence in diseases (Williams & Nesse, 1991, p. 8) as well documented empirical examples of group selection in nature. It is ironic that modern proponents of "individual selection" who think that they are operating in the tradition established by Williams have, in fact, departed from the framework that Williams actually defended. By interpreting both steps 1 and 2 as varieties of self interest, they have lost the ability to identify adaptation at the group level when it occurs.

HUMAN DECISION MAKING AND MULTILEVEL SELECTION

Decision making is a process whereby a course of action is chosen from a number of alternatives. The ability to make decisions is centrally related to fitness and therefore should be one of the primary functions of the human brain. Decision making provides an ideal subject for the study of multilevel selection in humans for a number of reasons. First, if the quality of the alternatives can be ranked, then the adaptedness of a decision-making process can be accurately measured by its success at choosing the best course of action. Second, decision making is not as internal as other cognitive processes because it involves so much gathering and evaluation of information from the environment. The mechanistic details are therefore relatively accessible to study (examples are provided later). Third, decision making has been a favorite topic of psychologists for decades, resulting in literally hundreds of empirical studies that can be used as a database for testing evolutionary hypotheses. Fourth, even when these empirical studies involve problems that are not closely related to fitness (e.g., evaluating job applicants), the ability of a decision-making process to solve any problem probably correlates highly with its ability to solve problems related to fitness. Fifth, there is a tradition of thinking about groups as adaptive units in social psychology that dates back to the founding fathers of the discipline, who freely speculated about "the group mind" (Durkheim, 1915; LeBon, 1903; McDougall, 1920; Ross, 1908; Wundt, 1907). The group-level perspective in psychology was largely replaced by a more individualistic view, as in evolutionary biology, but it was not totally eclipsed. As a result, there is a small but vigorous modern literature on decision making as an adaptive group-level process in humans.

To employ the multilevel framework, we must first try to imagine what human decision making would look like as a product of pure group selection (step 1) and pure individual selection (step 2).

Groups as Adaptive Decision-Making Units (Step 1). There are two senses in which human decision making can evolve to maximize the fitness of whole groups. First, individuals might function as independent decision makers whose goal is to benefit their group. This is the way that we usually think about altruism (Sober & Wilson, in press). Second, individuals might cease to function as independent decision makers and become part of a group-level cognitive structure in which the tasks of generating, evaluating, and choosing among alternatives are distributed among the members of the group. As with many other activities, decision making might benefit from the combined action, division of labor, and parallel processing made possible by groups of individuals interacting in a harmonious and coordinated fashion. At the extreme, the role of any individual in the decision-making process might become so limited that the group truly becomes the decision making unit, a group mind in every sense of the word.

The concept of a group mind is so strange, at least against the background of methodological individualism, that it may help to provide an example from nature. Social insect colonies such as honey bee hives are so highly organized at the group level that they can legitimately be called superorganisms (Seeley, 1989, 1996). To function adaptively, the hive must make decisions on almost a minute-by-minute basis 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 hive maintenance; and so on.

In an elegant series of experiments, Seeley and his colleagues have worked out in detail how some of these decisions are actually made (reviewed by Seeley, 1995). In one experiment, a colony with every bee individually marked was taken deep into the Adirondack woods where virtually no natural resources were available. The hive was then provided with artificial nectar sources whose quality could be experimentally manipulated. When the quality of a food patch was lowered below that of alternative patches, the hive responded within minutes by shifting workers away from the patch, yet individual bees visited only one patch and therefore had no frame of comparison. Instead, each individual contributed one link to a chain of events that allowed the comparison to be made at the hive level. Bees returning from the low-quality patch danced less and were less likely to revisit the patch themselves. With fewer bees returning from the poor resource, bees from better patches 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. Adaptive foraging decisions were made by a decentralized process in which individuals acted more as neurons than as decision-making agents in their own right. Even the physical architecture of the hive such as the location and dimensions of the dance floor, honey comb, and brood chambers has been shown to play an important role in the cognitive architecture of adaptive decision making at the group level.

Although the social insects help us to grasp the concept of a group mind, we should not expect group-level cognition in humans to resemble the social insects in every detail. In particular, individual humans are such sophisticated cognitive units in their own right that they are unlikely to become neuronlike even when they have become integrated into a single adaptive unit. It therefore may help to supplement the social insect version of the group mind with the following metaphor. Imagine a room containing 30 microcomputers. Ask the question, "How much could the computational power of these computers be increased by connecting them into a network with a sophisticated communication system?" It should be obvious that an integrated network of 30 computers will be vastly superior to 30 isolated computers. Some of the advantages of the network will be mundane, such as increased memory capacity, whereas other advantages will be more synergistic, such as parallel processing, division of labor, sophisticated error-checking mechanisms and so on.

Imagining the human group mind as an integrated network of computers does justice to the sophistication of the individual as a cognitive unit but still allows us to appreciate the network as a cognitive unit in its own right that is vastly superior to any single component. It also makes it obvious that the communication system connecting the computers and individuals must be highly sophisticated for the network to function efficiently and is unlikely to be acquired by domain-general learning and cultural mechanisms. If human cognition is a product of group selection, we should expect individuals to be innately prepared (Tooby & Cosmides, 1992) to easily "hook up" with other individuals to form an integrated cognitive network.

Thinking of human groups as adaptive decision-making units leads to many specific predictions about social organization, some of which will be outlined later (see also Caporall & Baron, chap. 12, this volume). These predictions may turn out to be right or wrong, but at least they provide a conceptual anchor, allowing us to recognize what adaptive groups would look like if they have evolved.

Individuals as Adaptive Decision Making Units (Step 2). If group selection can truly be ignored as a factor in human evolution, we should expect individuals to be highly adaptive as autonomous decision-making units, capable of performing the full range of activities from framing the problem, to generating alternatives, to evaluating the alternatives, to making the final decision. When individuals exist as members of groups, we should expect them to use others as sources of information, but only in ways that increase the individual's relative fitness within the group. We should not expect decisions that are adaptive for individual members to be necessarily adaptive for the group. Group-level benefits should occur only as the coincidental by-product of decisions that also maximize relative fitness within groups. After all, this is the entire thrust of Williams (1966). If "group-related adaptations do not, in fact, exist" (see passage quoted earlier), then regarding human groups as adaptive decision-making units is as wrongheaded as thinking that individuals evolve to benefit their species or that species evolve to benefit their ecosystem.

The same computer metaphor that allows us to imagine the human group mind as an integrated network also allows us to see why such networks can be undermined by within-group selection. Providing easy access to one's mind may be beneficial for the group, but it also makes one highly vulnerable to manipulation and exploitation by others within the same group. If the dangers of exploitation are sufficiently great, individuals should resist forming into adaptive decision-making units despite the advantages that all would share.

Determining the Balance Between Levels of Selection (Step 3). After we have imagined adaptive decision making at the group and individual levels, we must examine the factors that will determine where humans are likely to exist between the two extremes (step 3). At this point, it is important to appreciate that *Homo sapiens* is the most facultative species on earth and has existed in an enormous range of population structures throughout its evolutionary history. As a result, human decision making is unlikely to be located at a single point between the extremes. Rather, we might expect humans to have the capacity to function over the entire range, from autonomous decision-making units to components of a group-level mind, depending on the population structure in which they find themselves or build for themselves. We can also identify the kinds of groups in which adaptive group-level cognition will most likely be observed: groups with a high degree of genetic relatedness among the members, groups with a high degree of trust among the members, groups with social norms and other aspects of social organization that make exploitation within groups difficult, and groups in environmental situations that make the costs and benefits of group-level decision making large relative to the costs and benefits of exploitation within groups.

Once again, our computer metaphor provides an intuition about how human decision making might change along the continuum from extreme group level to extreme individual level functional organization. Imagine that you are an engineer who has built a computer network under the assumption that all of its users share a common goal. Then, to your dismay, you discover that some users are exploiting the network for their own gain, forcing you to implement features such as passwords and virus protection devices. The modified network is still useful, but not nearly as efficient as it was before, because the protection devices require resources and compromise the functional design of the network as a pure information processing device. Then, to your horror, you discover that those exploiting the network for their own gain are every bit as talented as you are and have discovered clever ways to bypass your defenses to plunder the other users. Ultimately you are forced to abandon the entire enterprise and sever all connections among the users. We must imagine human decision making as occupying this entire range of possibilities, from highly efficient networks that do not require protection, to compromised protected networks, to no networks at all.

Now that we have sketched steps 1 to 3 of the framework, we can evaluate the empirical literature on human decision making. To do this systematically, I employed the following procedure: First, I obtained the abstracts to 495 papers written between 1985 and 1994 by typing the keywords *group decision making* and *group problem solving* into the computerized literature service, Psych-Lit. The abstracts were downloaded and combined into a single file on my desktop computer. Second, all abstracts were read and summarized as short statements. Third, papers that address a specific topic (e.g., the effect of leader style) were found both by reviewing the statements and by using the "find" function on my word processor to locate appropriate key words (e.g., *leader*) in the file of full abstracts. Fourth, relevant papers were read in full along with other papers that they referenced. My ultimate goal is to test specific hypotheses that emerge from the multilevel framework with the formal methods of metaanalysis. In this article, however, space permits only an informal "guided tour" of research programs in psychology that are especially relevant to the evolutionary issues.

Individuals as Autonomous Decision Making Units

Individual humans do not always exist in groups, so they presumably have evolved to function as autonomous decision-making units in at least some situations. In a recent book entitled *The Adaptive Decision Maker,* Payne, Bettman, and Johnson (1993a; summarized in Payne, Bettman, & Johnson, 1993b) developed a research program that is highly conducive to the evolutionary perspective, even though the authors do not themselves relate their work to evolutionary theory. Payne and associates began by noting that there are many ways to evaluate and choose among alternative courses of action, which they called *alternative decision strategies*. For example, imagine that you are choosing among a number of habitats in which food, water, and safety from predators are all desirable attributes. One possibility is to evaluate each habitat for all three attributes, weighted appropriately, and then to choose the best habitat (the weighted additive strategy). Alternatively, you might first evaluate the habitats with respect to one attribute, evaluate the best of these for the second attribute, and so on (the elimination-by-aspects strategy). As a third possibility, you might simply choose the first habitat that exceeds an acceptable threshold for all three attributes (the satisficing strategy). Payne et al. identified six alternative decision strategies that tend to be used by human subjects.

Alternative decision strategies differ, not only in their ability to make good choices, but also in the time and cognitive effort that they require to work. The weighted additive strategy is the most accurate, but also the most costly, because all alternatives must be compared for all attributes that are weighted unequally. Because the adaptedness of a decision strategy depends on both its benefits (i.e., accuracy) and costs (i.e., time and cognitive effort), the most accurate strategy is not always the best. In fact, there is no single best strategy for all situations, and the adaptive decision maker must therefore have a collection of strategies that can be selectively employed in different decision environments.

Payne et al. measured the costs and benefits of the alternative decision strategies in impressive detail. They trained subjects to use all six strategies and to employ them in a computer-based information acquisition system called Mouselab. The subjects must use the mouse to acquire given pieces of information, allowing the computer to monitor the information they examined and the time they required to examine it (see Payne et al. 1993a for details). In this way, Payne et al. confirmed that the subjects were employing the prescribed strategy, the amount of time required to employ it, and the quality of their decisions.

To examine the cognitive effort required to employ a decision strategy, Payne et al. identified a number of elementary information processes (EIPs) that act as the building blocks for each strategy (Newell & Simon, 1972). Examples of EIPs include READ (read an alternative's value on an attribute into short-term memory), COMPARE (compare two alternatives on an attribute), and PRODUCT (weight one value by another). The cognitive effort required to employ a strategy in a given decision environment might depend on both the difficulty of each EIP (e.g., PRODUCT might be more difficult than COMPARE) and the number of times that each EIP is used. In addition, interaction effects might cause single EIPs to be more difficult in some strategies than in others. These possibilities were explored in a regression analysis that compared the number of each EIP used in a decision strategy as independent variables with response time and self-reports of effort by human subjects as dependent variables. The results suggest that the cognitive effort required to employ a decision strategy depends on the difficulty of the component EIPs and the number of times they are used, but not on interaction effects. In addition, subjects differed in the ease with which they could use single EIPs and therefore the effort required to employ a given decision strategy. This means that two individuals might adaptively employ different decision strategies in the same decision environment if their abilities to use single EIP's are sufficiently different.

The next step is to show that individuals can adaptively select the best decision strategy for a given decision environment. To determine what is the best decision strategy, Payne et al. modeled each of the six strategies as a production system (Newell & Simon, 1972) that combines the EIPs in a set of if-then rules that arrives at a decision. The production systems were then allowed to make decisions in Monte Carlo computer simulations and scored for both effort and accuracy. Finally, human subjects were confronted with the same decisions using MouseLab, and their choice of decision strategies was compared to the optimal strategies determined by the Monte Carlo simulations. In general, human subjects showed an impressive ability to select the appropriate decision strategy for a given decision environment.

Payne et al. (1993a, 1993b) provided an outstanding example of how the concept of adaptation can be used to inform the study of decision making as an individual-level process. However, they did not think about adaptation in the evolutionary sense and did not even use the word evolution in their book. This leaves a gaping hole in their research program. Where does all of this adaptive decision-making machinery come from? Payne et al. (1993b) addressed this question in a single sentence: "Individuals may have acquired different strategies through formal training or through experience" (p. 25). Evolutionary psychologists will immediately appreciate the inadequacy of this answer and how much the modular view of human cognition developed by Cosmides and Tooby (Cosmides & Tooby, 1992; Tooby & Cosmides, 1992) might add to the otherwise superb research of Payne et al. I return to the issue of innate mechanisms after discussing decision making as a group-level process.

Groups as Adaptive Decision-Making Units

If group selection has been an important force in human evolution, and if the process of decision making can benefit from coordinated action, then groups should make better decisions than individuals in at least some situations. As a newcomer to the psychological literature on decision making, I was struck by how many papers left the impression that groups are not effective decision making units compared to individuals. Yet, when I actually read the details of the studies, I discovered that groups frequently are much better than individuals at making decisions. It is important to explain this discrepancy and to establish the basic fact that groups can function as effective decision-making units before we proceed to the more detailed predictions of the multilevel framework.

Groupthink: Group Decisions as the Dysfunctional By-product of Internal Pressures. The concept of *groupthink* interprets group decision making as the largely dysfunctional by-product of internal forces (Janis, 1972, 1982):

> I use the term "groupthink" as a quick and easy way to refer to a mode of thinking that people engage in when they are deeply involved in a cohesive in-group, when

> the members' strivings for unanimity override their motivation to realistically appraise alternative courses of action.Groupthink refers to a deterioration of mental efficiency, reality testing and moral judgement that results from in-group pressures (p. 9).

Janis made several predictions that are consistent with the within-group selection view of human decision making (step 2) and diametrically opposed to the between-group selection view (step 1). If groups can function as adaptive decision makers, then highly cohesive groups are more likely to realize this potential than less cohesive groups (step 1), yet Janis predicted that groupthink is especially characteristic of cohesive groups because of in-group pressures (step 2). Group decision strategies should be most strongly favored in environmental situations that threaten the group as an entire unit (step 1), yet these are the very situations that contribute to groupthink according to Janis. At least some kinds of strong and charismatic leadership should contribute to group function (step 1), yet Janis predicts that they will make groups dysfunctional by limiting the influence of other group members and creating an illusion of invulnerability (step 2).

The concept of groupthink has become enormously influential in the social sciences in addition to becoming a household word. Janis's work was cited over 700 times in the *Social Sciences Citation Index* between January 1989 and June 1992 (Aldag & Fuller, 1993). Many social scientists that I have talked to have accepted the conclusion that humans are poorly equipped to make decisions in groups. In evolutionary terms, this would imply that human psychology has not been strongly influenced by group selection and that step 2 provides a more accurate image of human decision making than step 1.

The concept of groupthink is based on retrospective analyses of famous policy failures, such as the Bay of Pigs invasion, the Vietnam War, and the space shuttle Challenger accident . This approach relies on hindsight and qualitative assessment and needs to be verified with more systematic studies that compare the processes associated with good versus bad decisions. A number of laboratory studies and quantitative analyses of historical events have been performed, whose results force a revision in the groupthink concept. I will describe one study in detail because it shows how the decision-making processes of real groups functioning in their environments can be analyzed quantitatively.

Tetlock, Peterson, McGuire, Chang, and Feld (1992) developed a method known as the Group-Dynamic Q-sort (GDQS) for converting verbal historical accounts of decision making into a systematic form that can be compared across groups. The GDQS consists of 100 statements about the properties of groups that are printed on a stack of cards. A person who has read a historical account of a decision-making event sorts the cards into 9 categories depending on how well each statement describes the event. The number of cards that can be placed in each category is held constant, creating a unimodal distribution. Thus, the first category includes the 5 cards that best describe the event; the second category consists of the next 8 most descriptive cards, and so on to the ninth category, which includes the 5 least descriptive cards. Forcing the cards into a single distribution eliminates variation in the judgmental style of the sorter, such as the tendency of some individuals to make middle-of-the-road distinctions and of others to jump to extremes.

To analyze any particular decision-making event, at least three historical sources describing the event were identified. Two independent observers read and performed a Q-sort for each source separately, allowing correlations between raters and between sources to be separately assessed. The average correlation between raters was .83, which is comparable to the reliability of widely used psychological tests. The average correlation among sources describing a single historical event was lower (averaging .52) but still respectable. Thus, Tetlock et al. succeeded in developing a method for converting unsystematic historical accounts of decision-making groups into a form that allows their internal structure to be analyzed quantitatively, which is an important achievement. For example, with little modification it could be used to analyze anthropological accounts of decision making in tribal societies (Boehm, in press).

No decision-making process is guaranteed to achieve the best solution, and there might not even be a good solution to many problems confronted by groups. For example, the fact that the Vietnam war turned out badly does not necessarily mean that Lyndon Johnson and his team of advisors functioned poorly as a decision-making unit. The most negative assessment of the groupthink concept would be that there are no structural differences between the groups that Janis classified as groupthink and nongroupthink, based on the outcome of historical events. Tetlock et al. show that this pessimistic assessment is unwarranted. Most of the policy disasters discussed by Janis do, in fact, reveal structural deficiencies in the groups as decision-making units. For example, Johnson was clearly an overbearing leader who greeted dissenting views from his advisors with the ominous statement, "I'm afraid he's losing his effectiveness"(Janis, 1982, p. 115), forcing many to leave his inner circle and those who remained to suppress their criticisms. By contrast, the Marshall plan (categorized by Janis as an example of nongroupthink) was formulated in a period of three weeks by a leader (George Kennan) who deliberately encouraged discussion and disagreement among his advisors (McCauley, 1989, provided capsule summaries of these events in addition to a perceptive assessment of groupthink).

In addition to the policy disasters caused by dysfunctional groups, Tetlock et al. also discovered some exceptions to the rule. For example, the Mayaguez rescue mission during the Ford administration and the Iran rescue mission during the Carter administration were evidently formulated by groups that functioned well as decision-making units, but nevertheless failed because of bad luck. Of course, an imperfect correlation between process and outcome is exactly what we should expect for something as inherently stochastic as decision making.

Although Tetlock et al. show that there is something to the groupthink concept, they also show that Janis' account needs to be substantially revised. In particular, there is no evidence that group cohesion or the importance of the situation make groups less functional as decision-making units. On the contrary, cohesion and salience tend to enhance the performance of groups in decision making tasks. This conclusion has been reached by virtually every careful analysis of the groupthink concept, including qualitative assessments, quantitative analyses of historical events, and controlled studies that attempt to duplicate the conditions of groupthink in the laboratory. The most recent review (Aldag & Fuller, 1993) states it thus:

> On the basis of our review, it seems clear that there is little support for the full groupthink model. . . . Furthermore, the central variable of cohesiveness has not been found to play a consistent role. Flowers (1977) went so far as to state that "a revision of Janis's theory may be justified, one which would eliminate cohesiveness as a critical variable" (p. 895). This suggestion is diametrically opposed to Janis's (1982) view that high cohesiveness and an accompanying concurrence-seeking tendency that interferes with critical thinking are "the central features of groupthink." (p. 9)

We can summarize the groupthink literature from the standpoint of the multilevel selection framework as follows: Decision making at any level is a complex process that requires a number of components interacting in the right way to function properly. It would be astonishing if human groups always functioned as efficient decision-making units, regardless of their social organization. Furthermore, certain behaviors that obviously would increase relative fitness within a single group, such as leaders attempting to assert their social dominance, are especially likely to disrupt the ability of the group to function as an efficient decision-making unit. This illustrates the basic conflict between levels of selection, in which a group of individuals behaving adaptively does not make an adaptive group (Williams, 1966). If groups always behaved dysfunctionally as decision-making units, or were most likely to behave dysfunctionally in the very situations in which it is important to perform well (e.g., high cohesion, high salience), this would be powerful evidence that human mentality is largely the product of within-group selection. However, the groupthink literature does not warrant this conclusion. In fact, it provides compelling evidence for two of the basic ingredients of natural selection at the group level: phenotypic variation among groups in decision-making ability (step 3a) with important consequences for fitness (step 3c).

Benchmarks for Comparing Groups and Individuals. Psychologists tend to judge the decision-making ability of groups against a number of benchmarks, such as the ability of the average member acting alone (mean-of-*n*) or the ability of the best member acting alone (best-of-*n*). Often the purpose of a study is to demonstrate synergistic processes that cause groups to perform even better than the best individual, in which case the appropriate benchmark for comparison is best-of-*n*. Synergistic processes are highly interesting and are discussed below, but it is important to realize that they are not required for a decision-making process to count as adaptive at the group level. In fact, the distinction between within- versus between-group selection is different from either the mean-of-*n* or best-of-*n* benchmarks commonly employed by psychologists.

To see this, consider a group of individuals who vary in their knowledge about a particular subject that is required to make a good decision. If individuals are acting to maximize their relative fitness within groups (step 2), then experts should resist sharing their decision and the information on which it is based, causing the group to lie far below its best-of-*n* potential. We might even expect individuals to engage in sabotage by spreading false information, causing others to make even worse decisions than they would by themselves. This might appear dysfunctional to a psychologist (because the group lies below its mean-of-*n* potential) but an evolutionist would regard it as adaptive at the individual level. If individuals are acting to maximize the fitness of their group (step 1), we might expect them to actively meet to compare their private decisions and determine which is best if they do not all initially agree. The sharing of knowledge and joint evaluation of alternatives would eliminate fitness differences within groups and cause the group to approach its best-of-*n* potential. However, the group would not actually reach the best-of-*n* benchmark unless the most knowledgeable member can be determined with certainty. Furthermore, the group may well be unable to arrive at the best decision unless at least one member has reached it privately. This result might be a disappointment for a psychologist looking for synergistic effects (because the group fails to exceed its best-of-*n* potential), but it is gratifying for an evolutionist interested in adaptation at the group level.

When viewed from this perspective, the experimental evidence is overwhelming that groups usually exceed the decision-making ability of the average member (mean-of-*n* benchmark); they often approach and sometime exceed the decision-making ability of the best member (best-of-*n* benchmark). These results are especially remarkable because the vast majority of experiments were performed on extremely short-lived groups formed for the purposes of the experiment, whose members were complete strangers prior to group formation. If these minimal groups can outperform individuals, then the decision-making potential of real groups whose members are intimately familiar with each other might be very great indeed.

Two examples will illustrate how groups can surpass individuals in their decision-making ability, yet be judged as inferior to individuals by psychologists who employ a different set of benchmarks. Michaelsen, Watson, and Black (1989; see also Watson, Michaelsen, & Sharp, 1991) taught college courses in which students formed into learning groups that lasted the entire semester. The majority of class time was spent on group problem-solving tasks, including six objective and at least two essay exams that accounted for more than 50% of the course grade. Groups also met frequently outside of class to study and complete projects. This is one of the few research programs in which groups are presented with contextually relevant tasks and group dynamics have time to develop.

Exams were administered first to individuals and immediately afterward to groups (see Hill, 1982, for a discussion of this and other experimental designs in group decision research). In other words, after group members handed in their answer sheets, they were given an additional answer sheet to fill out as a group. For a total of 222 groups from 25 courses taught over a 5-year period, the mean individual test score was 74.2; the mean score of the best individual in each group was 82.6; and the mean group score was 89.9. A total of 215 groups (97%) outperformed their best member; four groups (2%) tied their best member; and three groups (1%) scored lower than their best member.

This study seems to provide overwhelming evidence for a group decision-making process that exceeds the best-of-*n* benchmark, but it has been criticized by Tindale and Larson (1992a, 1992b). The gist of their argument is that the best-of-*n* benchmark is exceeded only for the total test score and not for individual questions. If groups can do no better than select among the individual answers, and if all group members are wrong some of the time, then the best-of-n benchmark can only be approached at the level of single questions but can be exceeded at the level of the entire test. For Tindale and Larson, groups must be able to answer a question right *when every member answered it wrong* to demonstrate what they call assembly bonus effect.

Michaelsen, Watson, Schwartzkopf, and Black (1992) replied that their learning groups do display an assembly bonus effect, even as stringently defined by Tindale and Larson. From the multilevel perspective, however, even the most critical interpretation is good enough because it shows that groups can evaluate which of their members is most likely to be correct on a case-by-case basis. This error-checking capacity is available only to individuals who interact in cooperative groups.

My second example is the literature on brainstorming (reviewed by Mullen, Johnson, & Salas, 1991; Stoebe & Diehl, 1994), in which groups of individuals who suggest ideas to each other in a relaxed and uncritical atmosphere are supposed to be both more productive and more creative than individuals who attempt to generate ideas on their own. More than 50 psychological studies have compared the performance of brainstorming groups with the performance of so-called *nominal* groups, whose members generate ideas by themselves and do not interact with each other at all. The experimenter removes the redundant ideas generated by members of the nominal groups and compares their productivity and creativity with the brainstorming groups. These studies show unequivocally that brainstorming groups are less productive and are not more creative than nominal groups. The productivity loss of brainstorming groups is caused by a variety of factors involving both the motivation and coordination of group members. Ideas must be presented one at a time in the brainstorming groups, whereas individuals in the nominal groups can write their ideas simultaneously. Members of brainstorming groups can feel uncomfortable suggesting outlandish ideas despite their instructions to feel relaxed in front of each other. Standard social norms of politeness can prevent the most creative and productive individuals from taking over the brainstorming session (Stroebe & Diehl, 1994).

These studies definitely cast doubt on the magic spark of productivity and creativity that is sometimes claimed for brainstorming groups. From the multilevel perspective, however, brainstorming groups and nominal groups must be considered as two kinds of cooperative social organization. In one case the ideas are generated in isolation and then pooled for evaluation, whereas in the other case they are generated and pooled simultaneously. In both cases they are pooled, which means that individuals benefit from the ideas generated by other individuals. From the multilevel perspective, we need to compare the productivity and creativity of a single isolated individual, or a group whose members are attempting to maximize their relative fitness, with the productivity and creativity of a group whose members freely share their ideas. For example, consider an experiment in which many individuals are asked to generate ideas on a topic in isolation. It is possible that each individual can easily conceive of all the possibilities and that pooling ideas merely adds redundancy. If so, then the number of different ideas generated by nominal groups of size n should quickly plateau as n increases. Alternatively, if each individual can conceive of only a small fraction of the possibilities, then the number of different ideas generated by nominal groups will not plateau until large values of n are achieved. Figure 13.1 shows the results of one typical study (Bouchard & Hare, 1970; see Mullen, et al., 1991 for a review) which shows no hint of a plateau over the range of $n = 1 - 9$, for either nominal or brainstorming groups. If the number of ideas generated at the beginning of the decision-making process contributes to the quality of the final decision, there is little doubt that groups will surpass individuals; large groups will surpass small groups; and cooperative groups whose members freely share their ideas will surpass noncooperative groups whose members do not.

Multiple Group Decision Strategies. Just as individuals are faced with a range of decision environments that require an arsenal of decision strategies (Payne et al, 1993a, 1993b), so groups must have an arsenal of decision strategies to function as adaptive decision-making units (Steiner, 1972, 1976).

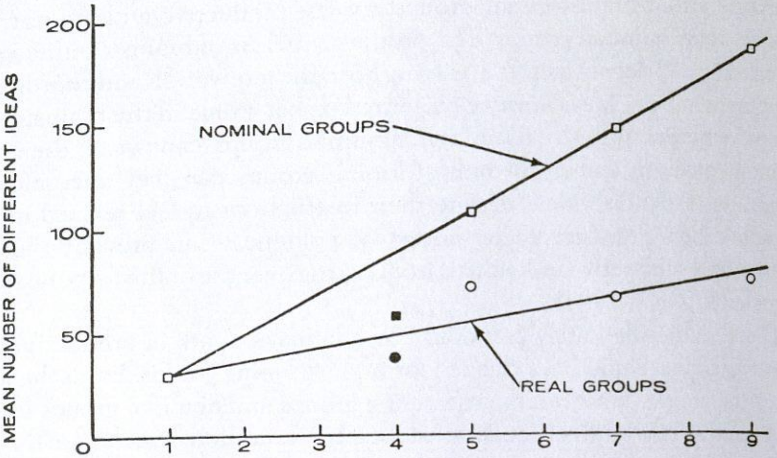

FIG. 13.1. The number of nonredundant ideas generated by brainstorming and nominal groups as a function of group size. From "Size, Performance, and Potential in Brainstorming Groups," by T. J. Bouchard and M. Haire, 1970, *Journal of Applied Psychology, 54*, p. 53. Copyright 1970 by American Psychological Association. Reprinted with permission.

The psychological literature is replete with examples of individuals who made stupid decisions because they employed the wrong heuristic, especially when the experiment caused them to frame the problem in the wrong way. We can expect the same kind of error at the group level. One interesting example involves a research program called *hidden profiles*, in which the information required to make the best decision is distributed among members of the group. Because individuals cannot get the right answer except by guessing, members of the group must interact synergistically to function adaptively. The first hidden profile studies suggested that groups do not perform better than individuals at this task. Members of the group seemed to focus on the information that they shared, which prevented them from integrating their unshared information. More recently, however, Stasser and Stewart (1992) distinguished between two decision-making strategies, only one of which is appropriate to the hidden profile task (see also Laughlin, 1980; Laughlin & Ellis, 1986). If the task is likely to have a demonstrably correct answer (an intellective task), then the appropriate strategy is to search until the answer is obtained. If the task does not have a demonstrably correct answer (a judgmental task), then the appropriate strategy is to reach a consensus. After all, if everyone is equally likely to be correct or incorrect, then the way to minimize error is to pool the estimates. Stasser and Stewart reasoned that groups perform poorly in the hidden profile task because they believe it is a judgmental problem rather than an intellective problem. They therefore changed the instructions to make it clear that the problem could be solved and obtained the results shown in Figure 13.2. Three factors were varied in a 2 x 2 x 2 design yielding eight treatments: (a) individual versus group, (b) "all shared" (all individuals receive all the clues) versus "hidden profile" (clues distributed among group members), and (c) subjects instructed that it is a judgemental task versus subjects instructed that it is an intellective task. Groups outperformed individuals in all conditions except hidden profile/judge. Groups who believed that they were solving an intellective task and had to merge their clues (groups/hidden profile/solve) performed as well as individuals who believed that they were solving an intellective task and were provided all the clues (individual/all shared/solve).

Groups as Decision Making Units in the Real World. Although the majority of psychological studies involve minimal groups that exist only for the purpose of the experiment, a few psychologists have made a special effort to study groups that actually function in the real world. Perhaps the most fascinating example is a recent book entitled *Cognition in the Wild* (Hutchins, 1995; see also Hutchins, 1991a, 1991b), which focused on the navigation methods of ancient and modern sailors. Unlike the decision-making tasks we have considered so far, that emphasize creativity and the solution of novel problems,

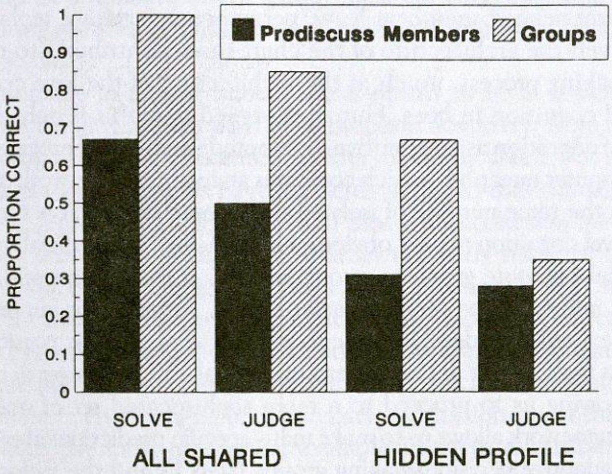

FIG. 13.2. The performance of individuals ("prediscuss members") and groups on a task in which the information was either available to all individuals ("all shared") or distributed among group members ("hidden profile") and the subjects believed that the problem was an judgmental task ("judge") or an intellective task ("solve"). From, "Discovery of Hidden Profiles by Decision-Making Groups: Solving a Problem Versus Making a Judgment," by G. Stasser and D. Stewart, 1992, *Journal of Personality and Social Psychology*, 63, p. 430. Copyright 1992 by American Psychological Association. Reprinted with permission.

estimating one's position on the earth's surface is a thoroughly routine procedure that must be performed again and again. Nevertheless, it involves a large number of decisions that are subject to error, with important consequences for fitness. When a boat is within sight of land, its position on a chart can be estimated by finding the compass directions of three landmarks, drawing lines from the landmarks on the chart at the appropriate angles, and noting where they intersect. The intersection of two lines is theoretically sufficient but does not provide an estimate of error. The intersection of three lines creates a triangle whose size indicates the likelihood of error.

On modern ships that are comfortably away from the shore, the entire task of estimating position is performed by a single person. When the ship enters a harbor, however, this person is replaced by a six-person team whose social organization has evolved over a period of centuries. Hutchins describes in detail how the team functions as an integrated cognitive unit, swiftly gathering and transforming information in a way that allows spatial position to be noted at a glance at three-minute intervals. The functional organization of the team includes a number of subtle but important design features. The members are spatially positioned and communicate in such a way that mistakes made by one person can be caught by at least one other person. There is redundancy of function so that the team can perform smoothly if one of its members is called away. The sequence in which the tasks are learned allows the team to function when its experienced members leave permanently and are replaced by new initiates. Even the architecture of the chart room contributes to the adaptive decision-making process, much as the architecture of the hive contributes to group-level cognition in bees. Hutchins argued that this is only one of many examples of cognition as an adaptive distributed group-level process in humans.

Our computer metaphor, which compares an integrated network of microcomputers with the same number of isolated microcomputers, makes the advantages of group-level cognition appear obvious. Nevertheless, a superficial reading of the psychological literature gives the strong impression that groups seldom function better than individuals as decision-making units. Because this impression is misleading, I devoted considerable space to asking the most basic possible question: "Can groups make better decisions than individuals?" The answer to this question is "yes," allowing us to proceed to a more sophisticated set of questions. The multilevel framework allows us to make many specific predictions about the design features of adaptive decision-making groups (step 1) and the factors that allow group-level organization to prevail over individual-level organization (step 3). Unfortunately, space permits the exploration of only a few of these factors.

Social Norms That Regulate the Group Decision Process

Decision making at any level is a complex process that requires multiple components working in a coordinated fashion to function well. This means that decision making at the group level requires a social organization whose structure can be predicted from the nature of the decision environment. Hutchins (1995) provided a good example for the case of navigation.

In many groups, the social organization required for adaptive decision making should be surrounded by a set of social norms that guide individuals through the process and make it difficult for them to subvert the process for their own gain. The details will depend on the decision environment. Adaptive norms governing groups attempting to solve a novel problem may be very different from adaptive norms governing groups attempting to solve a routine problem such as navigation. Nevertheless, a few generalizations can be made that furnish testable predictions.

Phase-Dependent Social Norms. Most decision-making processes require a sequence of phases, such as idea generation, idea evaluation, idea selection, and idea implementation (Aldag & Fuller, 1993). Because each phase requires a different set of activities, no single set of social norms can be optimal for the entire sequence. For example, pressures to conform may allow the group to act decisively (idea selection and implementation) but may inhibit the group from fully exploring the alternatives (idea generation). It follows that a really adaptive set of social norms must change dynamically as the decision-making process unfolds. Members of the group must be encouraged to be nonconformists during the idea generation stage, conformists during the idea selection stage, and so on.

Is it reasonable to expect human social norms to be as sophisticated and dynamically changing as they must be to function adaptively from the decision-making standpoint? This question is seldom explicitly asked, but at least some biologists and social scientists have implicitly assumed that the answer is "no." For example, Janis (1972, 1982) assumed that group cohesion inevitably leads to pressures to conform, which compromises the early stages of the decision-making process. Among biologists, Boyd and Richerson (1985) modeled conformity as an inflexible social norm that has an important effect on cultural evolution. Nevertheless, a number of studies in the psychological literature suggest that the social norms surrounding the decision-making process are phase dependent, encouraging both diversity and conformity at the appropriate times. Perhaps the most interesting example involves a naturalistic study of Israeli scout groups deciding between two sites for a work camp, one of which was clearly better than the other (Kruglanski & Webster, 1991). 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 the better (conformist) or worse (deviant) site, either early or late in the decision making process. After the decision was made, members were informed that their previous sociometric ratings had been lost and were asked to again fill out the same scale, enabling the experimenters to measure the social status of each member before and after the decision-making event. The only change in social status was a decrease that occurred when the confederate expressed a deviant opinion late in the decision-making process. This study provides clear evidence that social norms can be phase dependent, as they must to function adaptively at the group level.

Hierarchical Social Organization and Leader Control. In an early experiment, Guetzkow and Simon (1955) had members of five-person problem solving groups communicate with each other in a variety of ways. They found that the most efficient communication network was hierarchical, in which four members communicated directly with a central fifth member. More richly connected groups, in which all members could communicate with each other, were less efficient and actually reverted to the hierarchical structure over time by breaking some of the connections (see Collins & Raven, 1969 for a review of this research tradition). This study illustrates an important principle: Well designed information structures must often (although not always) be hierarchically organized (Simon, 1981). Purely from the standpoint of group fitness (step 1), we should often expect to find some individuals that we would call "leaders," others that we would call "followers," and so on.

Of course, social hierarchies can also be explained purely at the individual level, as the outcome of reproductive striving within groups (step 2). If individuals differ in their fighting ability, then the strongest will simply subjugate the weakest and take most of the resources. If the weakest are also the youngest, they might optimally bide their time as subordinate individuals until they grow large enough to challenge the dominants and so on. Thus, the multilevel framework provides two very different pictures of hierarchical social organization. Which picture best describes human groups and how they interact with each other when they both apply depends on the balance between levels of selection (step 3).

A systematic review of the psychological literature on leadership is beyond the scope of this chapter (see Bass, 1990; Hogan, Curphy, & Hogan, 1994), but at least two general conclusions seem warranted. First, when social hierarchies are required from the standpoint of group-level functional design, the conflict between levels of selection is likely to be severe because leaders, by definition, are in a position of power that allows them to exploit other members of their own group. For this reason, the social norms that control the behavior of leaders must be especially strong if the group is to function as an adaptive unit. There seems to be abundant evidence that leaders in human social groups are often controlled at least as much as they are in control (Boehm, 1982, 1993). They are selected on the basis of their ability to lead the group and are required to prove their leadership abilities by deed in addition to word. They are often required to take the same risks as other group members and are subject to exceptionally high moral standards. Often their power is confined to a single decision-making domain beyond which they have no special authority. None of these features of human leadership are expected on the basis of within-group selection and are easily interpreted as group-level adaptations. Of course, there is also abundant evidence that leaders frequently escape social control to exploit members of their own group. The point is that both steps 1 and 2 are required to explain the hierarchical nature of human groups.

Second, when adaptive group-level decision making requires a social hierarchy, the leader usually does not function as an autonomous decision maker who acts as the "brains" for the group. Decision making remains a group-level process in which the leader functions as a component. A study by Anderson and Balzer (1991) provides a good example, in which leaders of decision-making groups were instructed to announce their opinion either early or late in the decision-making process. The group generated more ideas when the leader's opinion was delayed and the final decision was often based on ideas that were not generated by the leader. In fact, a general rule for effective leadership from the group standpoint might be *act as an organizer and moderator of group-level processes and refrain from exercising too much personal control* (Hogan et al., 1994).

Innate Psychology, Learning, and Culture

The psychological literature on decision-making is remarkable for its lack of curiosity about where decision-making abilities come from, at either the group or individual level. The entire field seems to implicitly assume what Tooby and Cosmides (1992) referred to as the standard social science model (SSSM) in which all skills are learned from scratch by domain-general cognitive mechanisms. As an alternative to the SSSM, Tooby and Cosmides developed a view of human psychology in which the major activities that influenced fitness in ancestral environments, such as mate choice and social exchange, are governed by innate specialized cognitive modules that have evolved for millions of years. The human mind presumably consists of dozens of Darwinian algorithms invoked by environmental stimuli, much as a jukebox consists of many records played by pressing the appropriate buttons. Tooby and Cosmides realized that the mind seen as a juke box is as much a caricature as the mind seen as a single general-purpose computer, so the truth presumably lies somewhere between.

The study of human-decision making affords an excellent opportunity to explore the middle ground between these two extreme views of human psychology. The ability to make decisions is as central to biological fitness as mate choice, social exchange, and language acquisition, so there is every reason to expect it to be governed by innate specialized psychological mechanisms. It is impossible for an evolutionary psychologist to read Payne et al.'s (1993a, 1993b) account of multiple decision strategies without thinking of Tooby and Cosmides'

juke box metaphor. However, just because the six decision strategies st
Payne et al. function as modules does not imply that they are innate
One of the most fundamental conclusions that emerges from the decisi
ing literature is that adaptive decision strategies are as diverse as
environments (Steiner 1972, 1976), making it highly unlikely that a
Darwinian algorithm exists for every decision strategy. This does not m
we must abandon the jukebox metaphor entirely, but we do need to sup
it with more open-ended mechanisms of learning and cultural transmis
fine tune human decision-making ability to the particular decision
ment.

Adaptive decision making at the group level must similarly reflect a
of innate psychology, open-ended learning, and cultural transmissio
themselves can be guided by innate psychological mechanisms). Whe
my inquiry on this subject, numerous colleagues suggested that a revi
psychological literature was a waste of time because the study of minim
that exist only for the purpose of the experiment says nothing about the
or structure of real groups. It is true that real groups deserve far more a
from psychologists than they have received, but I am also impresse
information that has been forthcoming from minimal groups. It se
humans are innately prepared to function adaptively in groups under a
ate conditions and that learning and cultural transmission merely im
a scaffolding that is already present. A small literature exists on gro
decision making in children (French & Stright, 1991; Kinoshita, 1989
Joiner, Loveridge & Light, 1993), which may allow the appearance ar
opment of this scaffolding to be examined in more detail.

GENERAL IMPLICATIONS OF THE MULTILEVEL PERSPECTIVE

I have attempted to outline a general framework for thinking about m
evolution and to apply the framework to the specific subject of human
making. I conclude by discussing a few of the most important implica
the multilevel perspective for the disciplines of psychology, anthropol
evolutionary biology.

Implications for Psychology

It should be obvious that I regard the psychological literature as a gold
empirical information for testing evolutionary hypotheses about huma
ior. However, extracting this information is a bit like trying to assembl
jigsaw puzzle using the pieces from many small jigsaw puzzles. Dozens of
programs address specific issues (e.g., what accounts for production-blo

brainstorming experiments?), but in a larger sense they are conceptually adrift. A glance at some of the most general models of group decision making in the psychological literature reveals the nature of the problem. Aldag and Fuller (1993) separated the decision-making process into six compartments, each of which can be influenced by a large number of variables. For example, the compartment labeled *group structure* can be influenced by cohesiveness, homogeneity, insulation, leader impartiality, leader power, history of the group, probability of future interaction, stage of group development, and group type. The entire model includes 53 variables, which induces a sort of combinatorial paralysis. With 1,378 dyadic combinations and 23,426 triadic combinations of variables, where do we begin? Hirokawa and Johnson's (1989) general theory of group decision making also celebrates complexity without providing a guide for managing complexity.

The multilevel evolutionary framework is conceptually general and also appreciates the importance of multiple factors, but it leads to highly specific predictions that are not forthcoming from the other models. Steps 1 and 2 allow us to use the concept of functional design to predict exactly what adaptive decision making would look like if it had evolved at the group and individual levels respectively. Step 3 allows us to identify the major variables that will facilitate or disrupt adaptive decision making at the group level. Tooby and Cosmides' modular view of human psychology encourages us to look for cognitive foundations of decision-making abilities in a way that seems to have been almost entirely ignored by psychologists, if my sample of over 500 papers is representative. These elements of the multilevel framework act as guides for managing complexity by identifying specific regions of the parameter space that deserve attention. For example, relationships characterized by a high degree of trust should lie closest to the ideal of an integrated computational network (step 1) unburdened by the protective devices required in less trusting relationships. Individuals in trusting relationships should therefore be superior at decision making and other cognitive tasks. To my knowledge, this computational theory of intimate relationships has not been developed by psychologists interested in either decision making or intimate relationships (reviewed by Brehm 1992), with the notable exception of Wegner and his colleagues (Wegner, 1986; Wegner, Erber & Raymond, 1991; Wegner, Giuliano & Hertel, 1985) who explicitly adopt a group-level approach to human cognition. Thus, the multilevel framework easily locates an important region of the parameter space that has been previously missed by most psychologists.

Another major implication of the multilevel framework concerns the importance of studying human mentality as a group-level process. The concept of a group mind was popular among the first social psychologists, but was largely replaced by a more individualistic perspective, as in evolutionary biology. Those who continue to think about group-level cognition clearly regard themselves as endangered species within their own disciplines (Campbell, 1994; Hutchins,

1995; Wegner et al., 1985). The multilevel framework makes it obvious
the study of adaptive group-level processes needs to occupy a more cer
position in psychology. Thinking of groups as organisms is more than ju
metaphor. It is literally correct, to the extent that the traits being studied
the product of group selection. To say that adaptive group-level processes
merely the outcome of interactions among self-interested individuals is exa
as wrongheaded as saying that individual physiology is just the outcom
self-interested organs. The multilevel framework gives equal and equiva
status to individuals and groups as potentially adaptive units, which is a powe
justification for moving the study of group-level mentality to center stage
fact, in our modern world of books and computers, it is difficult for us to ima
how deeply communal human thought must have been throughout our ev
tionary history, when all knowledge had to be stored and passed between hu
heads (Ong, 1982).

The multilevel framework has implications for applied psychology in a
tion to that of basic psychology. Cognition at the individual level requ
communication among neurons. Cognition at the group level requires com
nication among individuals. Individuals must physically encounter each o
to communicate. Encounter rates are heavily influenced by the basic patt
of daily life and by the spatial architecture of buildings and villages. Wor
who wash their clothes together by a river will have more opportunit
communicate than women who wash their clothes by themselves in t
basements. I have witnessed numerous incidents in which an academic gr
such as a laboratory or a department moves from one building to another
experiences a radical change in its intellectual quality of life, usually for
worse. The new building causes individuals to bump into each other less of
and scheduled encounters (e.g., meetings) are not as effective as continu
and spontaneous encounters for certain kinds of communication. Thinkin
human mentality as a group-level process makes it obvious that mundane
pervasive aspects of human life, such as the placement of offices and
scheduling of activities, should be arranged to facilitate certain kinds of c
munication among members of a group. If architects and social plann
regarded themselves as group-level brain surgeons, perhaps they would th
in a way that results in fewer group-level lobotomies.

Implications for Anthropology

Anthropological studies have a special status in evolutionary psychology
cause they allow us to see how human behavior functions in environme
closer to the ancestral condition than our own modern world. It is there
important to know how well tribal societies (and especially hunter–gath
societies) function as adaptive decision-making units (Knauft, 1991). At
extreme, we might discover that tribal groups are best described by step 2 of

framework makes it obvious that
needs to occupy a more central
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t that the traits being studied are
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ters, it is difficult for us to imagine
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stored and passed between human

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of buildings and villages. Women
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ng units (Knauft, 1991). At one
are best described by step 2 of our

procedure and that group-level functional organization is a recent historical event. At the other extreme, we might discover tribal social organizations that are intricately adapted at the group level (step 1), including mechanisms that prevent individual-level selection within groups in the same way that the rules of meiosis prevent gene-level selection within individuals (step 3).

Boehm (1996) recently surveyed the ethnographic literature on the way tribal societies make decisions, especially in crisis situations. His main purpose was to show that decisions are often made by a rational process, as opposed to superstition or culturally determined traits inherited by simple transmission rules. For our purpose, his examples are remarkable for showing how decision making is functionally organized at the group level. Meggitt's (1977) description of Mae Enga raiding and warfare in highland New Guinea reads like a textbook example of nongroupthink. The major Big Man solicits responses from those present without offering his own opinion. All men who have passed through the bachelor's association are eligible to participate and, "being among their own clansmen, can speak with complete freedom." Anyone possessing pertinent information has "a moral obligation to contribute so that the group may reach the best possible decision in the circumstances." This procedure is followed because "only in this way, it is believed, can each clansman truly ascertain the thoughts of his fellows and the evidence behind them." The Big Men have their own opinion, but "none of them, especially in the early sessions, reveals much of his hand or tries patently to push for the acceptance of his suggestions." After hours of argument, a consensus usually emerges and the Big Man "incisively summarizes the main arguments, indicates which have been rejected, and finally announces the decision reached by the clan." Although freedom of expression is encouraged during the early stages of the decision-making process, the social norms eventually shift to favor conformity because "even as both parties are making clear their positions, everyone knows that, because the clan's survival may be at stake, once combat begins the doves will almost certainly take their places fighting alongside the hawks" (p. 76). All three examples of decision making reviewed by Boehm seem to lie remarkably close to the group-adapted end of the continuum (step 1). In another review article, Boehm (1993) showed that leaders of tribal groups are often highly controlled by their constituents, as expected for societies that are functionally organized at the group level.

Early anthropologists such as Evans-Prichard (1940/1979), and Levi-Strauss (1949/1969) speculated freely about social organizations and cultural practices that allow tribal groups to function as corporate units. For example, Evans-Prichard (1940/1979) described a segmented social organization for the Neur that allowed them to become functionally organized at a nested hierarchy of levels. Normally the smallest units in the hierarchy acted in a corporate fashion to accomplish the tasks of daily life but even these were large and genetically heterogeneous by biological standards. The smallest units fought among themselves but easily united into higher-level corporate units to fight other higher-level units. The only hint of social stratification was a person known as th leopard-skin chief, whose authority was limited to the single domain of conflic resolution. According to Evans-Prichard (1940/1979), "his function is politica for relations between political groups are regulated through him. His activitie are chiefly concerned with settlement of blood-feuds, for a feud cannot b settled without his intervention, and his political significance lies in this fac Chiefs sometimes prevent fights between communities by running between th two lines of combatants and hoeing up the earth here and there. The older me then try to restrain the youths and obtain a settlement of the dispute b discussion . . . On the whole, we may say that Nuer chiefs are sacred person but that their sacredness gives them no authority outside specific social situations . . . I have often heard remarks such as this: 'We took hold of them an gave them leopard skins and made them our chiefs to do the talking at sacrifice for homicide.'" (p. 173).

This way of thinking about tribal society is still common among anthropologists, but not among those who have been most influenced by evolutionar theory. Yet, it is highly compatible with step 1 of the multilevel framework. Thu viewing evolution as a multilevel process makes it even more relevant t anthropology than it has been so far.

Implications for Evolutionary Biology

Evolutionary biologists who regard themselves as individual selectionists overwhelmingly view nature (including human nature) through the lense of a individual organism attempting to maximize its inclusive fitness. This does no correspond to step 2 of the multilevel framework because the concept c inclusive fitness does not correspond to natural selection within single groups As Williams and Hamilton were among the first to appreciate (Hamilton, 1975 Williams & Williams, 1957), inclusive fitness theory assumes a multigrou population structure, with natural selection occurring both within and amon groups. Thus, even though modern individual selectionists think that they ar operating in the tradition of Williams and Hamilton, their concept of individua selection has been stretched to include elements of steps 1, 2, and 3 of th multilevel framework.

An article entitled "Group Composition: An Evolutionary Perspective (Harvey & Greene, 1981) provides a good example because it was published i a multidisciplinary volume on group cohesion (Kellerman, 1981) and therefor shows how evolutionary biologists have contributed to a subject that is relevan to group-level decision making. The paper begins with this statement: "Evolution through natural selection has produced patterns of group living amon animals that maximize the inclusive fitness of individuals" (p. 149). The author correctly define group selection as "natural selection operating on groups a opposed to individuals" (p. 151), but then immediately dismiss it as "theoreti cally feasible, but only under extreme conditions which are unlikely to be found in nature" (p. 151). Dominance hierarchies and other social structures are interpreted as follows:

> If we accept that animals modify their behavior in the presence of others for adaptive reasons . . . we might ask whether emergent social structures exist which cannot be reduced to an explanation at the individual level. The simple answer, from the adaptationist standpoint, must be *no*. For example, many social structures exist which have been described as emergent characteristics of group living, such as dominance hierarchies. But such arguments, when they provide any explanation of the existence of dominance hierarchies, rely on group selection. In animal societies, however, such social structures can profitably be analyzed in terms of individual reproductive strategies. Williams (1966) has pointed out that dominance hierarchies are no more than the "compromise made by each individual in its competition for food and mates, and other resources. . . ." (Harvey & Greene 1981, p. 163)

In this passage, Harvey and Greene seem to be explicitly denying the possibility that social hierarchies might function as decision making structures that benefit the whole group. The group-level speculations of early thinkers are described as follows:

> Evolutionary analyses of social form have frequently used the group as the unit of analysis, with a direct analogy to organic evolution in the formulation of society as a "superorganism". . . . For example, Bagehot (1872) argued that groups had a clear advantage over individuals in the struggle for survival, and that group cohesion was essential for group success. Gumplowicz (1885) continued this reasoning with strong group selectionist arguments—that social evolution proceeds through differential *group* survival. (Harvey & Greene, 1981, p. 164)

These passages sound for all the world as if Harvey and Green are employing the multilevel framework outlined earlier and are claiming that step 1 of the procedure should be avoided at all costs because group selection is such a weak evolutionary force. However, a more careful reading reveals that they have simply forgotten that Williams defined individual selection as natural selection within single groups. Their own conception of "individual evolutionary interests" includes a myriad of traits that do not increase relative fitness within groups and do require the differential fitness of groups to evolve, exactly as outlined by the early thinkers that Harvey and Green reject. In this way, group-level adaptations are barred from the front door but welcomed through the back door as a variety of self-interest.

There are two major problems with this conceptual framework. First, it is logically indefensible. If the tradition established by Williams is going to be followed, it should be followed well. Merely returning to Williams' own definitions of individual and group selection causes the modern concept of individua selection to collapse. Second, it is heuristically counterproductive. Group-leve adaptations are difficult to see when they are first explicitly denied and then accepted in a disguised form. To see them clearly, we must return to Williams original framework and ask the question that evolutionary biologists have avoided for so long: What would groups look like if group selection *were* the only force acting on them?

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VII

Capstone