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Small Groups From an Evolutionary Perspective

Linnda Caporael, David Sloan Wilson, Charlotte Hemelrijk, and Kennon M. Sheldon

Abstract

This chapter discusses evolutionary approaches to small group research. It defines basic assumptions of the evolutionary perspective and then demarcates major debates within evolutionary theory relevant to the social scientific study of groups. Four distinct evolutionary perspectives on groups are defined and compared. Results of evolutionary research regarding group composition, typical group sizes, group interaction, outcomes, and development and change in groups are reviewed. We conclude with a discussion of strengths and weaknesses of the perspective and directions that future research may take.

In research on evolution, the small group is something of an anomaly, located somewhere between genes and cultures. Our species has lived in groups throughout its existence and is descended from a long line of primate species that also lived in groups. Until very recently (in evolutionary terms), we lived in small groups that are somewhat approximated by hunter-gatherer societies (Boehm, 2000; Kelly, 1995). The advent of agriculture resulted in a transformation of human society over a period of only a few thousand years (Diamond, 1997). Because genetic evolution is a relatively slow process, in some respects, we are adapted to a physical and social environment with origins in the past. However, individual learning and cultural change can themselves be described as evolutionary processes, resulting in rapid adaptation to modern environments. Studying human groups from an evolutionary perspective need not be confined to genetic evolution (Boyd & Richerson, 1985; Dunbar, Knight, & Power, 1999; Durham, 1991).

Although there are some common themes, the study of groups from an evolutionary viewpoint is best classified as an emerging perspective. Some evolutionists question whether groups are real, whereas others see groups as central to understanding humanity and have attempted to derive theories of how groups evolved and the impact of groups on evolution. Although to one outside the field evolution may seem a cut and dried theory, the study of evolution is in fact full of debate and has many different positions. Evolutionary thought relevant to groups is so broad and diverse that it cannot be summarized in a short article. This chapter will attempt to give readers an introduction to key positions and debates and to some conclusions drawn in this emerging research area. In writing this chapter, we have chosen to elide many differences among the authors and encourage readers to seek out the references we cite to understand the particularities and differences among us.

In the next section, we will discuss some basic assumptions of evolutionary thought and debates relevant to the evolutionary view of groups. Following this, we will distinguish four alternative evolutionary viewpoints that differ in terms of their definition of group, the degree of importance they accord to groups in

the evolutionary process, and the specific aspects of groups they focus on. See [Table 10.1](#). Following this, we will summarize representative findings related to those of the seven questions guiding this book that evolutionary research has addressed.

Central Issues in Evolutionary Thought on Groups

The defining construct of evolutionary approaches is natural selection through variation, selection, and retention (for an accessible overview of evolutionary theory, including a brief discussion of evolutionary psychology, see Sterelny & Griffiths, 1999). Heritable variations serve as the raw material for evolution. Generally, variation is assumed to be random. Selection refers to the idea that those variations best adapted to their environment are more likely to survive, reproduce, and pass on their genes to future generations. Retention indicates that there must be a mechanism for preserving and passing on variations, that is, the gene. However, there are different schools of thought about what the proper unit of analysis is and how the evolutionary process occurs. We will discuss different positions advanced by evolutionary theorists and use them to lay the groundwork for understanding different approaches to understanding groups through an evolutionary lens (Hemelrijk, 2002a, 2002b).

Table 10.1 The Evolutionary Perspective

Definition of perspective	The evolutionary perspective does not constitute a single literature. There are diverse interpretations of Darwinism.
Key assumptions	<ul style="list-style-type: none"> • Adaptation (selection, variation, retention) • Two main approaches in human evolutionary theory: <ul style="list-style-type: none"> Historical: Adaptations to past circumstances produce psychological mechanisms for group living Functional: Groups are a by-product of individual behaviors to maximize reproductive potential
Types of groups	<ul style="list-style-type: none"> • Face-to-face groups • Nested hierarchy of groups: dyad, gossip group, primary network, intermediate group, tribe, societies
Key theories	<ul style="list-style-type: none"> • Machiavellian intelligence (gene's eye view) • Group selection • Coevolutionary theories • Niche construction
Dominant research methodologies	<ul style="list-style-type: none"> • Animal research (experimental and observational) • Conceptual analysis (philosophy of biology) • Historical/consilient research on human activities (war, religion) • Computer simulation and games
Strengths	<ul style="list-style-type: none"> • Potential to provide foundational principles on group structure • Potential to organize a large body of diverse findings about groups and provide novel hypotheses • New lens for understanding humans as fundamentally social beings
Weaknesses	<ul style="list-style-type: none"> • Very new area; widespread lack of integration across evolutionary perspectives, disciplines, vocabularies, acceptable research methods • Highly interactive with culture via high media profile and sociopolitical implications • Difficulty incorporating existing paleoanthropological evidence and lack of evidence about behavior in the past leads to multiple conceptual, theoretical, and methodological problems, including that the evolutionary past is not relevant

Not surprisingly, Charles Darwin (1859/1981) was the first to write about how groups might have shaped

human cognitive and social behavior. According to him, those tribes with the most sagacious of men would make the best tools, overcome their enemies, and have the most children, would increase in number and replace other less sagacious tribes. The moral faculties were more troublesome for this view. Sympathetic and benevolent parents, those willing to sacrifice their lives rather than betray their comrades, were less likely to leave offspring than were those less eager to enter the fray. But Darwin overcame this difficulty by positing the “love of praise” and “the dread of blame” as the stimulus to the social virtues.

A man who was not impelled by any deep, instinctive feeling, to sacrifice his life for the good of others, yet was roused to such actions by a sense of glory, would by his example excite the same wish for glory in other men, and would strengthen by exercise the noble feeling of admiration. He might thus do far more good to his tribe than by begetting offspring with a tendency to inherit his own high character. (p. 165)

Over generations, various factors would interact, resulting in the evolution of our “moral faculties.” These would not give even a slight advantage to the individual man in begetting children. However, a tribe possessing men with high degrees of patriotism, obedience, courage, and sympathy; ready to sacrifice themselves for the common good, “would be victorious over most other tribes; and this would be natural selection” (p. 166).

Fast-forward 100 years. Wynne-Edwards (1962) argued that individuals would curb their own reproduction to maintain stable population levels, the result of an evolutionary process he called group selection. A “strong” version of group selection holds that individual interests are subordinate to the collective interests of the group. Natural selection results from selection between groups rather than of individuals.

Williams (1966), however, argued that most apparent instances of group selection could be explained more parsimoniously in terms of benefit to the gene, meaning that more copies of the individual’s genes would be represented in succeeding generations. According to Williams, selection at the “genetic level” could readily explain altruism between relatives because helping one’s kin could mean that genes common to related individuals would benefit. Williams did admit, however, that human altruism might be an exception and speculated how it could evolve by group selection. Like Darwin, he agreed that there could be a “competition for goodwill” among unrelated individuals, and he imagined a primitive society where a good reputation based on altruism would pay off in terms of reciprocal exchanges, a theory later elaborated by Trivers (1971) as reciprocal altruism. Williams, however, concluded that apparent adaptations for group benefit would ultimately occur through the differential survival of individuals and would be designed for the perpetuation of the genes of the donor.

As the genes were the ultimate beneficiary, human altruism could not be considered an adaptation at the group level. By the 1970s, Williams’s (1966) book became the standard account of neo-Darwinism, the claim that the genes were the only relevant level of analysis for understanding natural selection. This position is often called “the gene’s eye view” or “the selfish gene” perspective.

The contrasting positions of Wynne-Edwards and Williams mark a debate important to evolutionary theories of groups. Most evolutionarily oriented psychologists follow Williams (1966) in rejecting group selection as an important force (Buss, 1999; Gaulin & McBurney, 2000), and groups are not even indexed in Barkow, Cosmides and Tooby’s (1992) well-known book, *The Adapted Mind*. Donald Campbell (1975, 1982, 1983; 1990b; Campbell & Gatewood, 1994) was a notable exception. He wrote on the conflict between individual and group interests, clique selfishness undermining superordinate collective goals, and groups as “vehicles” for shared knowledge, among many other evolutionary topics (Caporael, 2001b). Early on, Campbell believed that humans had innate altruistic motives (Campbell, 1965), but he later recanted this view. Convinced that the gene’s eye view supported the view of a basically selfish human nature, he argued that such self-interest was held in check by cultural norms that could evolve through cultural group selection (Campbell, 1975).

Wilson (Sober & Wilson, 1998; Wilson, 1975, 1983; Wilson & Sober, 1994) made the case that genes for altruism could increase in frequency as a result of selection at higher levels of organization, such as the group. Objections to the gene as the sole unit of selection grew out of the recognition that multilevel selection, which included group selection, was necessary for understanding the hierarchical and complex nature of biological phenomena (Buss, 1987; Maynard Smith & Szathmari, 1985). Wilson observed that self-sacrificial altruists will reproduce less than selfish egoists if the entire population is considered a single

group. However, if the population is composed of subgroups with varying frequencies of altruists and egoists, and if groups with more altruists outreproduce groups with more egoists, then even if the frequency of altruists relative to egoists within the group declines, the frequency of altruists in the whole population can increase. Other evolutionists also opposed the view that genes were the only level of selection for various reasons (Eldredge, 1985; Lickliter & Honeycutt, 2003).

The contrast between individual and multilevel selection views is complicated by the fact that there is considerable variability in the basic units of evolution. Units in different evolutionary theories include genes, organisms, groups, entities in general, organisms-in-settings, and by-products of self-organizing systems. Even the term *gene*, long regarded as a basic unit, is no longer a definitive construct: Dennett (1995) advises his readers to think of “virtual genes” if they feel squeamish about genetic determinism. That is, the basis of heritability may be more complex than bits of genetic code.

Frequently, the choice of a unit of selection corresponds to a particular theoretical position. The gene’s eye view points to genes (and sometimes individuals) as the unit of selection (Barkow et al., 1992; Buss, 1999). Groups plus other entities are associated with multilevel selection theories such as that described by Wilson and Sober (1994) and coevolutionary theories (Boyd & Richerson, 1985). Organisms-in-setting is a sign of constructionist approaches, which foreground the interactions of an organism and its immediate context as the unit of selection (Levins & Lewontin, 1985; Oyama, 1985). Systems and self-organizing approaches may combine all of the above units (Caporael & Baron, 1997; Hemelrijk, 2002a).

Theories may also vary with respect to how the concept of adaptation is used. Pan-adaptation is the assumption that a complex design results from natural selection. This is the widespread assumption in animal research, and there are advocates among human evolutionary theorists, as well (Barkow, 1989). In contrast, researchers on self-organizing systems posit that apparently complex social behavior may emerge interactively with only the simplest of rules built into an agent. Understanding how natural selection may operate on the products of such systems is one of the goals of this line of research (Hemelrijk, 1997; Latane & L’Herrou, 1996), which combines elements of adaptationist and emergent positions. These evolutionary approaches typically involve simulated agents (Hemelrijk, 1997) or situated robotics (Hendriks-Jansen, 1996).

Social Evolutionary Perspectives on Groups

Natural selection is a process that adapts organisms to their environments. For group living to evolve, the advantages would have to outweigh the disadvantages. Basically, individuals who grouped would have more offspring compared to individuals who lived solitary lives. Group living can be a hazardous to an animal’s health. Parasites and disease spread more easily in groups than among solitary critters. Competition for mates and resources can lead to injury and death. Plus, there is always the problem of free riders. Nevertheless, often, it is adaptive to live in groups, and an enormous diversity of groupings has evolved across the animal kingdom (Boinski & Garber, 2000). Some creatures are highly organized to function adaptively at the group level. Others are marked by conflicts of interest among their members. Evolutionary biologists have made considerable progress understanding the nature of animal groups. Almost all the same principles can be used to understand the nature of human groups, although there are disagreements. Some researchers see solitary living as a primal state and grouping as a deviation that requires explanation (Dunbar, 1989); others ask if groups are “real” rather than a perceptual/linguistic illusion (Palmer, Fredrickson, & Tilley, 1997); and still others insist that some types of group living—and humans are among these—cannot be derived from solitary states (Caporael, Dawes, Orbell, & van de Kragt, 1989). Social evolutionary perspectives on groups can be categorized into four approaches emphasizing the different ways in which the group construct is used. The categorization, however, is a matter of convenience. Grouping in nature is multidimensional; it changes over time and over life span, and as a function of resources and of reproductive states (Avital & Jablonka, 2000; Sussman & Chapman, 2004).

Groups as Aggregates

Quite often, sociality may consist of little more than a group of opportunistic and individualistic

cooperators (Norris & Schilt, 1988; Williams, 1966). A school of fish or a herd of fleet deer are aggregate groups. There may be safety in numbers, and the risks of predation might be spread out among a group of animals. As soon as the risks are reduced, the aggregate group breaks up. Some schools break up under the cover of darkness. African antelopes group when they live in the open, and they live solitary lives in forests where hiding is easier. Individuals that form opportunistic aggregates are adaptively specialized for knowing when to group and when to be solitary.

Groups are composed of interacting genetic competitors or rationally self-interested individuals. These approaches are common in evolutionary economics and evolutionary game theory, including studies modeling cooperation and competition (Axelrod, 1984, 1997; Gintis, 2000). Groups are viewed as aggregates of individuals (or dyads), with the assumption that the processes taking place in dyadic interaction scale up to large-group interaction. For example, cooperation in tit-for-tat games, which assume two players, is arguably a result of reciprocating behavioral control or feedback. A noncooperator on one round may be punished by her partner on the next when he fails to cooperate himself. Such control would be impossible in a large n -person game because the beneficiaries of cooperating activities may be spread out (giving rise to free riders).

“Players” in groups may also be categorized. In game theory, metaphors of “hawks” and “doves” may be used to describe the change in relative frequency of types in a structured game. In traditional evolutionary psychology (Buss, 1999; Tooby & Cosmides, 1992), groups may be based on gender or kinship. Many evolutionary researchers doubt that groups exist at all, arguing that their supposed entitativity is an artifact of human abilities to categorize (Palmer et al., 1997).

Cultural Evolution and Large-Scale Groups

Another approach incorporates culture as a crucial dimension for explaining human social behavior. The focus of interest is on human diversity as a function of the coevolution of both genetic and cultural influences. Durham (1976), for example, studied the distribution of adult lactose tolerance/intolerance (a biological trait) related to relying on milk and the use of milk products as a major source of nutrition (a cultural practice). The correspondence between long-term herding cultures and the ability to digest milk sugars illustrates the reciprocal relations between culture and genes. Such gene-culture coevolutionary theories do refer to subgroupings within a culture and to scenarios of prehistoric groups, but the focus is the application of evolutionary theory to explain within and between variations in societies.

Boyd and Richerson (1985) are well-known for elaborating gene-culture coevolutionary theories. In recent work, they argue that modern humans live in large-scale groups because of group selection on cultural variation, specifically, different institutional mechanisms that mimic small group living (Richerson & Boyd, 1999).

Self-Organizing Systems Approaches

There are a variety of systems approaches in evolutionary theorizing, all sharing an interest in self-organization and emergent interaction. In contrast to adaptationist approaches, which assume complex behavior must be influenced by genes inside the organism, self-organizing systems approaches start with computer models of agents (organisms) that are controlled by a few simple behavioral rules and obtain knowledge of their nearby environment only—in contrast to attaining global knowledge by individuals, as is assumed in optimality models. The challenge is to build “bottom up” models in which complex behavior emerges from simple organisms. The collection of agents themselves is “the group.” Although the agents interact with their environment and other agents, their behavior is studied in the same way as in ethology. Results show that in these models, very simple agents generate complex social structures and that the same set of rules may lead to different patterns, depending on the past experience of different individuals, the demography of the population, or the distribution of food. There are few studies of the effects of self-organization in humans so far, but there are many such studies of insects and artificial systems (see Hemelrijk, 2002b, for a review).

Systems approaches challenge the implicitly accepted idea of “evolved complex mechanisms” with a parsimonious perspective that may turn out to be more appropriate for the human behavioral sciences. Instead of genes carrying the burden of explanation for complex behavior, simple behavioral rules or forms may

evolve, with complex behavior and structure emerging as a product of interaction between the organism and the local environment. Such interactive emergence can be observed in artificial systems such as situated robotics (Hendriks-Jansen, 1996) and in real life (Thelen & Smith, 1994).

Small Group Models

Most explanations for the evolution of sociality have to do with defense from predators or cooperative foraging. But there can be other advantages to group living (Avital & Jablonka, 2000). Group members may learn vicariously about features of the local habitat such as locations for food. Slow-growing offspring may have special tutors and guards. Food may be regurgitated and shared. Some species even learn behavioral traditions exploiting novel resources. A common bird in Britain, the great tit, is famous for having learned to open the lids on milk bottles (when they were commonly delivered to people's front doors), a behavior that spread throughout the country.

There are other kinds of groups that cannot break up. The individuals that form such groups *must* be part of a group in order to reproduce and for the young to survive to reproductive age and start the cycle again. These groups are *obligately social* groups. They organize individual efforts and communication within the group, and they have tasks and roles for group members, as well as definable group boundaries (Brewer, 1997). In extreme cases such as wolf packs, naked mole rats, and meerkats (a social mongoose), only a breeding couple reproduce. Other group members contribute to the survival of the offspring.

In the human case, any work appealing to hunter-gatherer groups and ancestral environments could be said to have small groups as the basis of a model of human groups. However, surprisingly few models focus explicitly on the structural features of small groups and their connection to the evolution of social behavior or their relevance for large-scale groups.

The best known is Dunbar's (1993) work on the coevolution of language, neocortical size, and group size (summarized later). Boehm (2000) is also concerned with small groups; his interest in them is as the source of egalitarianism. Caporael (1997) problematizes the small group, theorizing how groups exist and coordinate behavior at all. Evolutionary perspectives on small groups also appear in management science. Campbell (1974, 1990a, 1994) influenced this work, which uses evolution either as a metaphor for institutional change or as an explanation for small group behavior (Baum & McKelvey, 1999).

The distinctions among these four positions are somewhat arbitrary and many studies could be classified into more than one category. However, they suggest the considerable diversity in disciplines and approaches to small groups from an evolutionary perspective, from claims that groups are not real to claims that individuals may be components of group "super-organisms." The following section summarizes evolutionary studies that address some of the seven basic questions that illustrate principles and thinking from diverse perspectives. In this section, we include relevant examples from studies of both human and nonhuman species. Comparisons across species, a tradition that was more common during past decades of psychological research than at present, can help convey the continuity and the complexity of evolutionary processes and outcomes. It might seem that by focusing on ancient environments, long-term evolution, and other species, the evolutionary perspective is only marginally relevant to the study of modern human groups. However, evolutionary thinking looks to the long term, and we believe the ensuing discussion will contribute to the same range of subjects and issues addressed by other perspectives on groups in the social sciences.

Results of Evolutionary Research on Small Groups

Evolutionary approaches to groups have not addressed all seven questions posed in this volume evenly. Evolutionary research naturally tends to emphasize questions related to the nature of individuals and their interrelationships in groups; how typical groups such as families, clans, and tribes influenced human evolution; the role of evolution in the creation of norms; the evolution of prosocial behavior and conflict; and groups as environments for individual evolution. See [Table 10.2](#) for a summary of findings relevant to the seven questions.

Table 10.2 Key Findings of Evolutionary Perspective Research

Group composition	<ul style="list-style-type: none"> • Kin and unrelated reciprocating individuals in face-to-face groups • Group size • Artificial agents • Nonhuman animals
Group structure	<ul style="list-style-type: none"> • Aggregates of minimally interacting actors or agents • Face-to-face groups in core configurations • Emergent group structures (e.g., dominance hierarchies) • Enormous between-species variability in group structures
Group projects	<ul style="list-style-type: none"> • Interface with habitat • Maximizing reproductive success
Interaction	<ul style="list-style-type: none"> • Conflict and cooperation • Clique selfishness • Imitation, social learning, and social control
Group action/outcomes	<ul style="list-style-type: none"> • Reproduction and survival to reproductive age • Coordination of activity and information transfer • Norms
Change over time	<ul style="list-style-type: none"> • Natural selection (variation, retention, selection) • Ontogeny • Cultural transmission and evolution
Ecology	<ul style="list-style-type: none"> • Groups serve as interface between individual and habitat • Niche construction (Organisms create and are shaped by niches resulting from organismic activity.) • Culture

Group Composition

Evolutionary studies have emphasized kinship, family role, and gender and their demographic distributions within groups as key variables affecting group interaction and thereby influencing adaptation and selection processes. Group size has also been a central object of interest.

In much evolutionary research, groups are taken for granted as a background against which social exchange, alliances, competition, mating, and other activities are played out. In traditional evolutionary psychology, environmental considerations such as the structure of relationships become important insofar as they identify adaptive problems and, therefore, hypotheses about cognitive design. This means that group attributes, specifically group attributes in the ancestral environment where human cognitive mechanisms evolved, are characteristically treated as independent variables, whereas cognitive design and associated characteristics are the dependent variables.

In the gene's eye view of evolution, performance is associated with reproduction, and interaction is frequently discussed in terms of altruism as opposed to self-interest. Kinship is a key factor of group composition in traditional evolutionary psychology. In general, groups pose different adaptive problems and opportunities for their individual members. Kin-based groups provide better opportunities for cooperative activities than do groups of unrelated individuals because individuals share, on average, copies of genes. Hence, human psychology is theoretically adapted to behave differently in different group contexts. We would expect distinct mechanisms for dealing with kin (and, indeed, for different kinds of kin), with mixed-sex groups, with all-male groups, and so forth. Geary (1998) provides an overall gene's-eye-view model of the mind in terms of mechanisms responsive to group categories. Considering the different kinds of individuals people might have encountered in the "environment of evolutionary adaptedness" (the environment in which selection for an adaptive trait actually occurred) can offer a good clue toward considering adaptive design. An important part of the gene's-eye view is that evolved psychology should reflect all and only those collections of individuals that recurred over evolutionary time. For example,

adaptations for parental investment indicate that mothers (and fathers) and their offspring were together during long periods of their lives. Similarly, because the costs of assuming strangers are friendly when in fact they are hostile are likely to be far greater than the benefits lost from assuming strangers are unfriendly when they are not, we should expect particular caution with respect to strangers—in its extreme form, xenophobia.

Gender and age figure prominently in almost all evolutionary approaches, although with the exception of warfare (discussed later), there are few theories relevant to groups where gender and age are considered as demographic factors. In a study of primates by Hemelrijk and Luteijn (1998), the quality of social relationships was found to depend on the demographic distribution of males and females. It appears that female relationships are better (as measured by the degree of reciprocation of grooming among females) when there are relatively more males present among the adult members of the group. Females reciprocate grooming in proportion to the relative number of males that are present per female in the group. Reciprocation among females is weaker when there are fewer males per female. This is explained as a consequence of the intensity of competition among females for access to males. This competition is stronger if there are fewer males per female in a group, and in such a case, the quality of social relationships among females decreases.

The sex ratio of groups of primates, however, does not influence female relationships in groups of all species. It only influences female relationships in species in which females remain resident for the rest of their lives in their natal group. It does not hold for other species in which females migrate once they have become adult. This is understandable because in such female-transfer groups, instead of competing for access to males among themselves, females have the alternative option of simply finding males elsewhere.

Demography may influence the dominance structure of a group, particularly how youngsters may acquire high social rank or dominance. Datta (1992) developed a model showing that in fast-growing populations of primates (such as macaques), newborn female infants are protected by all family members against attacks by anyone (also other family members). Therefore, female infants have a higher dominance position than older sisters. In slowly growing populations, however, such protection is lacking due to the absence of sisters, and therefore, each individual fights for itself, and dominance positions are acquired in accordance with the fighting abilities of individual females.

Group size is another composition variable that has received much attention in evolutionary research. Group size is much easier to study in smaller, short-lived organisms than in primates, and research suggests size is implicated in fairly complex relationships. In ants, group size determines whether one or more of equidistant food sources of equal quality are exploited. If the group size is large, the colony exploits a single food source rather than many (Nicolis & Deneubourg, 1999), whereas small groups tend to exploit several food sources equally. The cause of this is that in large groups, the pheromonal reinforcement of the marking of a trail to a specific food source is much stronger than in small groups. This leads to greater uniformity in food exploitation.

In view of the common assumption among evolutionary researchers that humans have spent much of their evolutionary history in hunter-gatherer groups, it is somewhat surprising that there are not more theories specifically concerned with group size. Dyads are easily the most commonly studied interaction groups, deriving from work in evolutionary game theory (Lewontin, 1961; Trivers, 1971). Nevertheless, an important outcome of the game theory work is that humans are found to be far more cooperative than traditional notions of rational self-interest or selfish genes would suggest (Gintis, 2000). Social psychological research suggests that the level of analysis may be crucial for predicting competition. Insko and his colleagues show that groups are more competitive than individuals and that intergroup competition is stronger than intragroup competition (Wildschut, Pinter, Vevea, Insko, & Schopler, 2003).

Although most theories of groups can be classified as economic models of grouping, two similar theories are more specifically concerned with group structure. Dunbar (1993) and Caporael (1995, 1997) independently advanced models of typical group sizes that have evolved in human society. Dunbar identifies four group sizes that seem to represent typical groupings: gossip groups comprising two to four individuals, primary networks made up of bands of 30 to 50 individuals, intermediate groups of 100 to 200 individuals (corresponding to a village or lineage), and tribes of 500 to 2,500 individuals (the latter may be influenced by colonialism). Dunbar shows a correlation between mean group size and relative neocortical volume for several nonhuman primate species and argues that the same regression function underestimates human neocortical size, indicating that neocortical size is larger than would be expected on the basis of primate

group size. In his view, gossip groups represent a shift in the evolution of humans from servicing social relationships with grooming, as is common in primates, to servicing them with useful information about the behavior of others in the groups.

Caporael (1995, 1997) proposes a model of face-to-face group structure with core subgroup configurations based on considerations of group size and modal tasks. Subgroup size and task requirements are used to jointly specify dominant forms of group interaction. For example, a dyad is a core configuration with a size of two and modal tasks that include interaction with an infant. A core configuration is an environment where certain capacities, such as finely tuned microcoordination (as used in interactional synchrony), can evolve. The other configurations are teams, demes, and macrodemes, analogous to the foraging parties, bands, and macrobands in anthropology. The basic hypothesis is that aspects of mental systems should correspond to features of modal tasks characteristic to configurations, which in turn are grounded in morphology and ecology. Caporael suggests that the core configuration model can explain previously unrelated findings in social psychology such as movement synchronies, distributed cognition, and social identity.

Group Structure

Evolutionary research has also addressed the issue of how group structures, particularly norms, develop and affect the evolutionary process.

One common way of viewing group structure from an evolutionary perspective is at the population level. This is done by considering the initial frequency distribution of the alternative genes in the population and modeling change over time in the distribution based on selection coefficients favoring one over the other. The genes are in individuals in a group, and the selection coefficients may or may not include the effects of interaction among individuals. These processes are also modeled using evolutionary games as an analogy to the analysis of population structure (both begin with binary processes as in coin flips). The games typically consist of two strategies, such as hawk and dove, and a payoff matrix motivates the interactions of the actors playing the strategies. Such games may highlight frequency-dependent selection, which is an effect of the group on the individual and arguably a type of group selection (Sober, 1984). Trivers' (1971) well-known work on the evolution of reciprocal altruism is based on the Prisoner's Dilemma. The matrix structure is such that it can promote cooperation, given low costs for helping, the ability to remember the source of aid, and future opportunities for reciprocation.

In gene-culture evolution theories, there may be little discussion of goal-oriented groups, but there are certainly implicit assumptions. For example, the imitation of practices and values is important in cultural evolution (Boyd & Richerson, 1985; Durham, 1991). Imitation is neither random nor passive. Rather various evolved decision rules, such as "copy the successful" or "copy the prestigious," bias what cultural variants are imitated and become more frequent in the culture. Norms and values evolve in this fashion.

Humans far surpass other animals in their use of culture and norms to guide behavior. According to Boehm (2000), human social groups are remarkable for the balance of power among their individual members, a balance that is achieved by effective coalitions against would-be alpha males. Such coalitions also occur among chimpanzees and baboons. The result is a form of guarded egalitarianism in which self-serving behaviors of all sorts are largely suppressed and the group behaves largely as a coordinated unit. If this scenario is correct, the ability to establish and enforce norms is part of a continuum between humans and nonhuman primates. One crucial difference between humans and nonhuman primates is that human cultural change is cumulative, one innovation providing the basis for subsequent innovations, which has not been observed in any other species (Tomasello, 1999). It is, therefore, a matter of contention whether the major features of human cultures and norms can still be explained within the framework of a gene-based version of the evolutionary approach.

The concept of human groups as moral communities (where morality is defined as "conformance to the rules of right conduct") has important implications for cultural transmission (Wilson, 2002). Behavioral variation can exist both between individuals within social groups and between social groups in a larger population. Differences between groups are often difficult to achieve and maintain when behaviors are coded directly by genes. However, cultural mechanisms reinforced by norms can cause even large groups to become behaviorally different from each other, and the same mechanisms maintain the differences despite the

movement of individuals among groups (who abandon the customs of the old group and acquire the customs of the new group). Because natural selection is based on behavioral variation regardless of whether it is genetic or cultural in origin, norms and culturally acquired traits can result in forms of evolutionary change that could never happen by genetic evolution alone. Once again, these possibilities are best explored by thinking of culture and norms in conjunction with biological evolution rather than as a mysterious and ill-defined alternative (Boyd & Richerson, 1985; Wilson, 2002). So, for example, the tendencies to form and follow norms may be thought of as coevolutionary adaptations that contribute to complex cultural organizations and differentiations.

The study of culture and norms from an evolutionary perspective is relevant not only to the “big picture” of human evolution but also to the dynamics of social groups in everyday life. Social identity theory shows how easily people think of themselves as members of groups, especially in opposition to other groups (Abrams & Hogg, 1999). Social dilemma experiments demonstrate the fragility of cooperation in the absence of punishment but the ease with which it is achieved when the opportunity for punishment is allowed (e.g., Ostrom, Gardner, & Walker, 1994). A book aptly entitled *Order Without Law* (Ellickson, 1991) shows how people in small groups spontaneously establish, enforce, and largely abide by social norms in the absence of a formal legal system. Toqueville (1835/1990), the French social theorist who observed American democracy with such insight over a century ago, was equally perceptive about small-scale social groups in general when he said that “the village or township is the only association which is so perfectly natural that, wherever a number of men are collected, it seems to constitute itself” (p. 60). There is great opportunity for a synthesis between evolutionary biology and other perspectives in the social sciences to explain the mechanisms that people employ so naturally when they form into groups.

Hierarchical structure is another recurrent theme in the evolutionary perspective on groups. Dunbar (1993, 1996) and Caporael (1995, 1997) propose that groups are structured as a nested hierarchy of subgroups. Combining their two schemes, the dyad is nested within gossip groups, which are nested within primary networks, which are nested within intermediate groups, which are nested within tribes. Baum and Rao (2004) advance a theory of organization-environment coevolution as a nested hierarchy of evolutionary processes. Boyd and Richerson (1985) adopt a similar hierarchical structure in their argument that complex societies have a segmentary hierarchy. Although such hierarchies may have been functional in earlier phases of prehistory, they lead to inefficiencies in complex societies where subgroups subvert larger group goals, and changes of command are necessarily remote and lack the personal charisma of a leader.

Group Interaction

Humans engage in a number of group activities, including warfare and intergroup conflict; a range of cooperative activities, including hunting and mutual defense; and cooperative child-rearing, including care from distantly related or even unrelated group members.

Research on interaction such as conflict and prosocial behavior makes up a large part of the research involving evolutionary perspectives on social behavior. Most often, the group context is taken for granted, and theorizing is applied to “groups in general,” which could include very large groups or populations. Nevertheless, interaction processes for groups in general must be based on cognitive mechanisms evolved and developed in small group contexts and then extended to larger groups. Research on prosocial behavior illustrates this type of work.

Prosocial behavior is a complex construct. At the behavioral level, this includes helping others in myriad ways, sometimes at a cost to oneself. At the psychological level, it includes wanting to help others as an end in itself, even the abandonment of self-will encouraged by many religions (Batson, 1991; Sober & Wilson, 1998; Wilson, 2002). At the social-structural level, it includes social systems that constrain people to behave prosocially whether they want to or not. For example, according to Rawls (1971), a just society is one that a person would design for him- or herself, subject to the constraint that the designer will be placed randomly within it. Such a society requires checks and balances to withstand the inevitable presence of antisocial behavior, which is adaptive to the individual in some contexts.

To pick a single example, males of many species have evolved to kill infants that are not their own offspring, which makes the mothers of the infants available for mating (Van Schaik & Janson, 2000). Males and females of the same species have evolved to protect their offspring, but they are not always successful.

This is a clear example of how evolution can lead to conflicts of interest, behaviors that are bad for the group, and even individuals who act prosocially in some contexts (males protecting their own young) and antisocially in others (the same males attempting to kill the young of others).

All of these elements of prosociality can plausibly evolve through genetic and cultural evolution. In general, prosociality evolves when prosocial individuals manage to confine their interactions to each other, either avoiding antisocial individuals or withholding benefits from those who cannot be avoided. This general condition can be satisfied by many mechanisms that operate more or less strongly across the animal kingdom. Genetic relatedness constitutes one important mechanism. If helping has a genetic basis, then a genetic relative of a helper is also likely to be a helper, compared to an individual chosen at random from the population. Conversely, a genetic relative of a nonhelper is also more likely than chance to be a nonhelper. When relatives interact with each other, prosocial individuals become partially segregated from antisocial individuals automatically. This reasoning leads to a theory of nepotism (prosocial behaviors directed toward genetic relatives) that applies to humans and other species alike (Hamilton, 1964, 1975).

Other mechanisms allow tendencies toward prosocial behaviors to evolve among genetically unrelated individuals. If unrelated individuals learn each other's propensity to help, the helpers can form friendships with each other and force the nonhelpers to live a solitary existence or to interact with each other by default (Wilson & Dugatkin, 1997). If nonhelpers cannot be avoided, then conditional behavioral strategies can evolve that direct helpfulness toward helpers and unhelpfulness toward nonhelpers (Axelrod, 1984; Dugatkin, 1997). Some of these mechanisms require a degree of cognitive sophistication (e.g., the ability to remember individuals and their past interactions), which may explain why our own species employs them so successfully.

Efforts to foster prosociality are more likely to succeed by providing the conditions that make prosocial behavior successful than by divorcing it from an evolutionary context. One example will illustrate how these ideas can be used to guide social science research on small human groups. In a recent study of American college students (Sheldon, Sheldon, & Osbaldiston, 2000), newly arrived freshmen were given a questionnaire measuring their degree of helpfulness. Primary participants were asked to select three friends or acquaintances (secondary participants) to fill out the questionnaire, with the understanding that there was also a game embedded in the questionnaire, a game with prizes. In the questionnaire, all participants completed the values measure (which yielded a significant intraclass correlation—*assortation* on the basis of values), and all made bids in 5 one-shot social dilemma games (i.e., with no feedback regarding the choices of other group members).

Participants could win prizes either by choosing to increase their individual point score (defect) or by increasing the group point score (cooperate). Game scores were then computed for each person, with reference to the participant's associated group members' bids. Although those with more prosocial values lost points within their groups, this disadvantage was mitigated by the fact that their groups as a whole were more cooperative: Those within more prosocial groups tended to receive higher individual game scores than those in less prosocial groups. The net advantage of prosociality depends on the degree to which prosocial individuals can recognize each other and form cooperating groups. The degree of assortation on shared values after a few months of college was weak—at 0.18—as far as correlations go, but it can be loosely compared to measures of shared genes (a proxy measure of shared values) where genealogical relatedness with first cousins is 0.25. Established human groups with a longer history of interactions presumably exhibit an even greater degree of assortation, although this needs to be tested. More research is needed to establish the psychological and social-structural mechanisms that increase prosocial assortation in an effort to make them work better.

The other side of the coin of prosocial behavior is conflict and warfare. For traditional evolutionary psychologists, outgroups are a continuing feature of the ancestral past and, consequently, some argue, so is warfare. In particular, the cognitive mechanisms that underlie intergroup conflict are believed to contribute to inclusive fitness. Warfare is in particular need of explanation because although between-group conflicts lead to within-group benefits, individuals' private interests are not self-evidently served by engaging in them. The costs of participating in intergroup conflict are high, possibly the cost of life, and a share of within-group benefits is likely to be less than the risks. Humans are unusual in that they form nonkin, male-based

coalitions that engage in group-level cooperative activities. In particular, humans, across cultures and time, fight wars involving substantial numbers of individuals (Chagnon, 1988; Keegan, 1993; Tiger, 1969; Wrangham & Peterson, 1996).

A feature of warfare is that males involved in the conflict often rape females of the opposing group, to the winners' reproductive advantage. It has been argued that warfare is a result of adaptations specifically designed to facilitate ingroup cooperation for the purpose of outgroup exploitation. Tooby and Cosmides (1992) have argued that there is a domain-specific *coalitional psychology* specifically designed to solve the adaptive problems associated with intergroup conflict. A critical feature of this argument is that male reproductive success is limited by access to females. This model assumes that the reproductive benefits of warfare offset the potential costs, leading to a psychology of intergroup aggression. The widespread association between warfare and rape is consistent with this idea (Kurzban & Leary, 2001) as well as with other non-evolutionary explanations.

Two other important forms of group interaction are coordination and information transfer. Some animal studies are illustrative of evolutionary findings on these forms. Female guppies (*Poecilia reticulata*) have innate preferences for certain male characteristics such as body size and coloration. However, if a female guppy is allowed to observe another female choose one male over another, she develops a preference for the chosen male and others like him. This copying behavior is sufficiently strong to override the female's own innate preference. Remarkably, younger females copy older females but not the reverse (Dugatkin, 2000). Information transfer may also occur without direct imitation. For example, well-fed rats are neophobic; they resist foods with novel tastes and smells. Nutritionally stressed rats are neophilic; they sample novel foods and gradually incorporate those that do not make them sick into their diet. However, even a well-fed rat will be neophilic if it smells the novel food on the muzzle of another rat (discussed from an evolutionary perspective by Gaulin & McBurney, 2000). Rhesus monkeys sometimes give a call when they find food, bringing other monkeys to the scene. Hauser (1992) claims that if one monkey observes another fail to call after finding food, the former is likely to aggressively attack the latter. More generally, one reason that animals are highly sensitive to rewards and punishments in the laboratory is because in their natural competition, their fights among themselves can be seen as a kind of punishment, and incidental tolerance or grooming (in primates) can be seen as a possible form of reward.

The aforementioned examples clearly bear a resemblance to the acquisition and enforcement of behaviors that we associate with culture and norms in our own species, but they can be fully understood as biologically evolved adaptations. Other individuals are a rich source of information that can be obtained at lower cost than by interacting directly with the environment. Modifying the behavior of others with rewards and punishments can be highly advantageous. Thinking of culture and norms as coevolved adaptations in their own right, rather than alternatives to biology allows us to identify design features that might be missed otherwise. For example, accepting a new food only when smelled on the muzzle of another rat makes perfect sense from an adaptive standpoint. Similarly, in human societies, finding that another group member has already accepted a belief seems to heighten the attractiveness of that idea for those who newly encounter it.

Outcomes

By definition, successful group action results in survival and development to reproductive age of the individuals in the group. Shoaling, for example, leads to protection of group members (e.g., Landeau & Terborgh, 1986; Neil & Cullen, 1974). Among humans, if group action is unsuccessful, if there are too many unavoidable egoists, if wars and other intergroup conflicts are lost, then the minimal conditions for survival, reproduction, and development to reproductive age fail to be sustained, and the group and (less frequently) all its constituent members perish. The vulnerability of isolated humans or small groups of humans almost requires the concept of cultural group selection to explain why humans have been able to persist.

Time and Change

Time has several meanings for evolutionists—geological time, historical time, and lifetime. For the small hunter-gathering type groups of human prehistory, there would have been (ecologically dependent) minimal group size for the group to be self-sustaining. There would also have been maximum group size, constrained

by ecological resources, and, according to several researchers, cognitive constraints as well (Caporael, 1995; Dunbar, 1993; Richerson & Boyd, 1999). The formation of subgroups in Caporael's (1997; Caporael & Baron, 1997) core configuration model is an ongoing dynamic process embedded in everyday task demands and activity. Groups form with respect to a task, dissolve, and reform for other tasks. Over evolutionary and cultural scales of time, groups form through the fissioning of large groups into smaller groups, with the development of the group being this activity sustained through generations.

From a historical perspective, the beginning of large-scale ultrasociality probably starts with settlements of related groups and the elaboration of nested hierarchy with cross-cutting group relationships. Urban life still has these elements, although overlaid with bureaucratic, efficiency-minded structures (that typically fail to achieve the promised efficiencies). Group fissioning still occurs in groups that have some freedom for self-organization such as scientists (Hull, 1988) and religious groups (Olsen, 1987).

Ecology and Environment

From a traditional evolutionary perspective, one meaning of ecology is a reference to the concept of the "environment of evolutionary adaptedness," that is, the ancestral past to which human minds are adapted. Some evolutionary psychologists believe that because humans now live in a world radically changed, human behavior may be maladapted. In contrast, human behavioral ecologists (Smith, Mulder, & Hill, 2001) argue that human behavior is adaptive (fitness maximizing) in current ecologies.

Another meaning of ecology refers to the role of the environment in natural selection. As we mentioned previously, self-organizing systems and natural selection via adaptation are sometimes thought of as opposing perspectives. However, self-organization and natural selection may work together, as illustrated in the following example (Hemelrijk, 2002b). In certain populations of a species, food scarcity may lead to an increase in the intensity of aggression via natural selection on the level of the individual because more intensely aggressive individuals are better able to grab the food. Environmental feedback from the spatial positioning of individuals of different dominance positions leads by self-organization to a steeper dominance hierarchy. This may be advantageous at a group level because during food scarcity, despotic societies may survive better than egalitarian ones because at least some females get enough food to reproduce, whereas in egalitarian societies, due to the equal division of food, none of the females can get sufficient food to reproduce. The difference between the two types of groups sets up the conditions for group selection. Under conditions of scarcity, egalitarian groups are likely to fail compared to despotic groups, where some limited reproduction continues to occur.

Conclusion and Future Directions

No single evolutionist would agree with our description and assessment of the evolutionary perspective on groups; indeed, none of the authors of this chapter are in complete agreement, either. Nevertheless, all are committed to the notion that an evolutionary approach merits more discussion and exploration. One strength of the evolutionary approach is in its potential to serve as a unifying theory and as a hybrid science across a wide variety of disciplines and methodological strategies (Caporael, 2001a). Where many other perspectives, such as the functional perspective, must qualify claims based on the type of task involved, the evolutionary perspective offers an explanation that is, for the most part, independent of the specific tasks a group performs. Because the evolutionary explanation is seated in human genetics and coevolved features of culture that are invariant across situations (e.g., prosociality), it offers explanations that are potentially more powerful than many other perspectives on groups.

The evolutionary perspective also shifts groups to front and center of understanding human psychology and social behavior generally (Caporael 2001a). Humans cannot survive and reproduce in the absence of a group. Human mental systems have evolved in groups, and we should expect that further research on groups from an evolutionary perspective will reveal a great deal about the mind that will be unexpected. At minimum, evolutionary theory can function as an imagination pump, back story, or standpoint on which to

motivate middle-level theory and research. The last facility, however, also points to a weakness in evolutionary theorizing, and that is its well-known capacity to lend itself to evolutionary storytelling (Caporael, 1994; Kuper, 1988; Maynard Smith, 1987).

Issues to be resolved include questions about the grain of evolved traits. Should we expect them to be tightly integrated, large-grain capacities such as coalitional psychology, child rearing, or mate finding (Tooby & Cosmides, 1992)? Or are evolved traits largely small-grained, with components more like Lego blocks (Bechtel, 2003; Sher, 2003) that can be integrated through coevolutionary processes or by culture into many larger grain patterns, including a variety of group structures, functions, and activities? An analogy would be to several abilities (reading, bicycling, driving) that seem to be smaller-grained capacities available to be culturally reorganized. The issue of grain underlies questions about the flexibility of behavior in general.

Future directions for evolutionary perspectives on groups will have to include greater attention to the relations between theory and research. Basically, genetical evolutionary theory is one where the dependent variable—relative reproductive success of an alternative trait relative to other such traits—cannot be easily measured for human social traits. (The main independent variable—gene sequences for the trait in question—are not that measurable, either.) Although lab experiments and surveys done in the name of evolution have produced some interesting results, they may be more explicable in terms of media influence and current custom rather than Darwinism. A coevolutionary view of mind and culture removes issues of genetic determinism at the same time it muddies the waters. Little is known about how culture and biology come together to shape mental life or group life. Against these issues is the greater problem that the time scale of natural groups can be very long.

Overcoming these obstacles compels an interdisciplinary effort marked with substantial goodwill and intellectual generosity. Evolutionary approaches to groups will require new mixed-method, multimodel approaches (Tashakkori & Teddlie, 2003). These would include field observation, ethnography, computer simulations, focused experiments, and even robotic simulations. Despite the many challenges, however, the emerging evolutionary perspective promises a rich field of inquiry about fundamental properties of groups and mind.

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A Framework for Comparing Premises of Nine Integrative Perspectives on Groups

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Abstract

This chapter considers the nine perspectives with respect to a set of generic features that we refer to as touchstones. We ask what each of the perspectives says about: (1) the entity itself (i.e., group), including its formation and composition; (2) the context or setting within which that entity is embedded (i.e., issues regarding its boundaries and external influences on it); (3) the processes that take place in the group, both interaction patterns among members (e.g., interdependence, regulation of action) and psychological processes of members (e.g., cognitive, emotional, intentional); (4) the emergent properties, patterns, and/or outcomes of group existence and action; and (5) causality. Those comparisons show considerable similarity among various perspectives, as well as marked contrasts among others. The resulting picture of nine complementary but overlapping perspectives presents a much richer and more extensive picture of groups than any one of them alone.

The scope of this volume is awesome. Each chapter individually covers a vast terrain, and in combination, they demarcate the truly expansive domain of theory and research on groups. This is a unique, far-reaching, and quite remarkable compendium.

We undertook the daunting task of trying to compare and contrast the nine perspectives on the basis of a smaller set of features. Our intent was to select what seemed to be essential features of the content domain, but stated at an abstract or “meta” level. Inevitably, the inclusion and exclusion of features are to some degree biased by our own personal perspectives.

One key challenge has been that no reference points are truly ontology-free in themselves. Thus, the fit of the framework we employ to the complete set of perspectives is by nature less than perfect—fitting some ontological assumptions better than others. Nevertheless, we have tried to use these features as touchstones—referents against which each tradition may be compared and analyzed. (The term *touchstone* refers to a black stone that was used in ancient times to test for gold and silver by rubbing the purported rare metal stone against it.) We hope researchers will find that our touchstones offer additional insights.

Our presentation is organized around five major touchstones:

1. The Entity: How is the group formed and composed?
2. Context: How is the group situated with respect to group boundaries and to interaction with its external environment?