Conflict in Organizational Groups
New Directions in Theory and Practice

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Chapter 5

SELECTIVE CONSEQUENCES OF WAR

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ABSTRACT

Deadly intergroup conflict—war—appears to have been a persistent characteristic of our ancestral past. Using a computational model, we explore how the selective pressures of warfare may have shaped the human propensity for behaviors that benefit one's own group at an individual cost. We distinguish between two types of altruistic behavior: heroism, the propensity to risk injury or death by fighting on behalf of one's group, and communitarianism, the propensity to provide nonmilitary assistance to fellow in-group members, again at some cost to oneself. Our model explores how the asymmetric consequences of war for winners and losers and the possible contributions of communitarianism and heroism toward winning wars may have shaped the evolution of both classes of behavior. Results suggest that even infrequent war can promote the evolution of heroism, but that communitarianism is promoted only in the context of constant war and when group size is small. We discuss how cognitive and behavioral adaptations to recurrent intergroup conflict over millennia may be relevant to group conflict in the twenty-first century.

INTRODUCTION

A group of seafaring people settle on a previously uninhabited volcanic island that provides all the resources needed for survival: fresh water, fertile land for crops, trees for fuel, and attractive sites for rock shelters near protected bays rich in marine life. The settlers build stone-walled terraces to improve the land for agriculture, and stone fish traps harness the tide to provide protein for a growing population.
Fast forward a few hundred years. The island is now densely populated by descendants of the original settlers, and the trees are gone. The rock shelters near the bays have been abandoned. The islanders now live in fortified settlements on the top of rocky peaks in communities numbering from around 25 to perhaps a few hundred people each. Although they are far from the fields and bays, exposed to the weather, and inconvenient in other ways, the new settlements provide a commanding view of the surrounding area. Ditches, walls, and high ground offer obvious military advantages over the seaside rock shelters, and archaeological evidence and ethnographic accounts indicate that some older communities have been completely exterminated. Settlement patterns have been reorganized to cope with deadly intergroup conflict.

Rapa, the island in this tale (Kennett, Anderson, Prebble, Conte, and Southon, 2006), is located in the South Pacific, a region that has inspired Western fantasies of earthly paradise from Gauguin to Margaret Mead. Paradise is a fleeting phenomenon, however, easily degraded by crowding, resource stress, and war. The pattern is evident throughout Polynesia, where warfare is rare among founding populations of islands but increases through time with demographic expansion and increased competition for resources (Kennett, Anderson, and Winterhalder, 2006; Kirch, 1984). Archaeological evidence suggests that this deadly pattern was a recurrent feature of our species’ prehistory (Keeley, 1997; LeBlanc and Register, 2003; see Fry, 2006 for a contrasting perspective). In this chapter, we explore some possible consequences of resource conflicts and war in shaping how humans behave in groups.

Our species has a demonstrated ability to survive in a wide variety of habitats, from savannah to remote islands, from dense forest to arctic tundra, to cities and industrial organizations. One feature that has remained constant across space and time, however, is the context that humans take with them wherever they migrate and that shapes whatever institutions they devise: the human social group. Group living is likely the oldest and most stable feature of the changing environment in which humans and our hominid ancestors evolved and to which we are adapted, and groups are still the context for much of the activity that takes place in modern organizations. Like the inhabitants of Rapa, but on more compressed timescales, groups in organizations can also transition from periods of peaceful focus on productive work to periods of intense intergroup conflict. The transition back to a peaceful regime is much harder to achieve, whether in a modern organization or on a remote island. Why?

We believe that it is difficult to find a way out of intense intergroup conflict regimes in part because such conflict activates cognitive and behavioral propensities that were shaped by war, that are evoked by cues associated with war, and that have helped our ancestors—both recent and remote—adapt successfully to a social environment in which conflict with other groups can threaten the survival of the groups involved. In this chapter, we report on a project that uses a computational model to explore the possible role of warfare in shaping the evolution of two such behavioral propensities. Both are forms of evolutionary altruism (Sober and Wilson, 1998) that
benefit one's in-group at some cost to oneself. We distinguish between communitarianism, which refers to costly actions that benefit other in-group members in the context of intragroup dynamics, and heroism, which refers to actions that expose oneself to danger to benefit the group as a whole in the context of intergroup conflict. By investigating different forms of altruistic behavior in the same model, we seek to investigate whether or not they may have evolved by the same route.

Note that we use these particular terms to refer only to those behaviors that come at an individual cost. Everyday behavior includes a wide array of prosocial actions that are not individually costly, and people may also benefit personally from attacking others who happen to be out-group members. Such actions do not pose a conflict of interest between individual and group, and they are not the focus of our chapter.

Group interaction does, however, routinely pose conflicts of interest between what is best for the group and what is best for the individual—between group-serving and self-serving courses of action. This tension among choices to cooperate or defect is familiar across the literature of the social sciences (for example, Axelrod, 1997; Weber, Kopelman, and Messick, 2004). People differ in how often and under what circumstances they act in a way that serves the collective interest, but without some willingness to curb one's immediate self-interest and do what is best for the group, human well-being and survival are threatened. Concern for the collective outcomes of others in such conflicts of interest typically stops short at the boundary of one's own in-group, however, and the same people who are willing to (with some frequency) put aside immediate self-interest to benefit fellow in-group members may seek to actively harm out-group members.

From the perspective of the in-group, these behaviors are not contradictory as long as they target in-group and out-group members respectively. Abundant evidence documents the sensitivity of humans to in-group and out-group membership cues (for example, Schaller and Conway, 2001; Stangor, Lynch, Duan, and Glass, 1992; Turner, 1987; Wilder, 1986). The tendency of intergroup relations to be much less cooperative than interpersonal relations is well established (Pemberton, Insko, and Schopler, 1996; Wildschut, Pinter, Vevea, Insko, and Schopler, 2003), and the discontinuity can go beyond simple failure to cooperate to active aggression (for example, Meier and Hinsz, 2004; Sherif, Harvey, White, Hood, and Sherif, 1961).

When group members are threatened with danger, people may act altruistically to protect the group by injuring or killing others. In contemporary state societies, this role is played by the police officer or soldier. In smaller-scale societies, it is the job of the warrior—a role that may be required of most or even all able-bodied adult males. From this perspective, helping to build a fish trap that will benefit everyone (in-group cooperation) rather than defecting by letting others build it and free-riding on their efforts, and fighting neighbors (intergroup hostility) rather than fleeing or hiding and letting others fight on one's behalf, can both be considered forms of altruism,
although the behaviors themselves (helping, harming) look quite different and are likely based on different subsets of cognitive and motivational components.

Fighting for one's group at the risk of serious injury or death is thus conceptually equivalent to other altruistic behaviors that benefit others at a personal cost. Of course, societies can arrange for successful warriors to reap fitness benefits as compensation via, for example, higher status or access to women (for example, Chagnon, 1988; Junker, 1999; Patton, 2000). These rewards can adjust the cost/benefit ratio so that heroism is no longer altruistic in an evolutionary sense, regardless of the proximal individual motivations that drive behavior (Eibl-Eibesfeldt, 1979; Tooby and Cosinides, 1988). Warriors who die, of course, forego any fitness rewards, and warriors who manage to avoid the greatest dangers could presumably reap the benefits due to warriors while the more courageous perish. The rewards a given warrior does or does not reap depend on the outcome (live, die, sustain serious injury) for a particular conflict. Whatever the results for the individual, however, the group stands to benefit from a warrior's contribution.

Societies in which group-benefiting behaviors are rewarded are more likely to prosper than those that lack such reward systems, which can result in a form of cultural selection among groups known as equilibrium selection (Boone, 1998; Boyd and Richerson, 1990; Miller, 2000). Before these reinforcement systems are established, however, the behavior has to develop in the first place, and in advance of these cultural adjustments, we need to explain how behavior that is evolutionarily altruistic could initially emerge.

A growing literature studies contexts in which people negotiate simultaneous conflicts of interest within and between groups (for example, Bornstein, 1994; Rornstein, Kugler, and Zamir, 2005; Goren, 2001). We, too, are interested in the interplay between mixed-motive conflicts of interest between individuals and the groups to which they belong (Schelling, 1960) and in conflicts of interest among groups that seek to exploit the same finite resources.

We believe that recurrent intergroup violence—war—may promote the resolution of such conflicts of interest in favor of one's group. Whether such resolutions are viewed as having positive or negative effects depends on both temporal and contextual frames of reference. Behfar and Thompson (chapter 1, this volume) distinguish between within-group and between-group forms of conflict and among functional, dysfunctional, and quasifunctional perspectives depending on whether conflict is viewed as positive, negative, or mixed in its results. Like many scholars who study conflict, we are interested in the results of conflict. Our primary interest is on ultimate results over a long time frame (evolutionary history) rather than proximate results of particular conflicts, although proximate results (winning or losing a war) are part of the engine that drive the process of evolution in our model.

We believe that an evolutionary perspective may help check the common tendency of scholars to assume that intergroup conflict is necessarily dysfunctional, overlooking how it might (from the perspective of a group rather than a society or
organization) serve the interests of those involved (in other words, how it might be functional or quasifunctional in the terms set out in chapter 1).

We proceed as follows. First, we consider the role of war in evolution. After reviewing evidence that war has exerted selective pressure on human groups, we explain the logic of multilevel selection and how it might apply to war and group-serving behavior. Second, we describe our computational model and present some results that show how group size and cost/benefit structures may affect the evolution of heroism and communitarianism. We conclude by discussing some possible implications of our thinking about human adaptation to war for understanding conflict-related cognition and behavior in contemporary groups.

THE ROLE OF WAR IN EVOLUTION

THE SELECTIVE PRESSURES OF WAR

Any major source of death can operate as an agent of selection, and war appears to fit this criterion. Archaeological (for example, Keeley, 1997; LeBlanc and Register, 2003) and anthropological (for example, Chagnon, 1974; Ross, 1984) evidence suggests that our ancestral past was characterized by persistent coalitional violence with significant mortality rates. Estimated death rates (Keeley, 1997, p. 196) from prehistoric data range from as high as 48 percent for males and 45 percent for females for a site in Nubia dating to 10,000 before the common era (BCE) to more modest rates such as 8 percent overall mortality (men, women, and children) from Brittany in 6,000 BCE (see, however, Fry, 2006). Going further back in prehistory, remains are too fragmentary to allow credible estimates of relative mortality or to distinguish between murder and war as causes of death. However, evidence of interpersonal violence and cannibalism dates as far back as the period during which the genus Homo was first emerging (see Walker, 2001, for a recent review of the bioarchaeological evidence).

Contemporary hunter/gatherer societies, believed to provide the closest analogues for much of the evolutionary past of Homo sapiens, have death rates ranging from the relatively low (but nontrivial) 8.3 percent overall mortality for the Gebusi (Knauf, 1985) to highs of 59 percent male, 27 percent female mortality for the Jivaros (Ross, 1984) and 37 percent male, 4 percent female for the Yanomomo (Chagnon, 1974). Male/female asymmetries in death rates are also evident in genocidal conflicts playing out today. Refugees streaming out of the western Sudanese province of Darfur are being fed and sheltered in camps that are 90 percent women and children; the men and older boys in these families have almost all been killed or captured or are otherwise missing (Pelley, 2005).

Substantial male mortality rates from intergroup violence have also been documented for some bands of common chimpanzees, Pan troglodytes (Wilson and
Wrangham, 2003), suggesting that acts of war (including raiding and opportunistic killing of out-group members) have plausibly been exerting selective pressure since before the branching off of hominids and chimpanzees from our common primate ancestor roughly five million years ago.

Along with a tendency for war to kill more males than females, the outcomes of war exhibit other important asymmetries. One is the advantage of attackers over defenders, especially for raids and ambushes, the most common form of combat in hunter/orager societies (LeBlanc and Register, 2003). This is also the form of coaltional violence practiced by common chimps (Wrangham and Peterson, 1996). Raids are designed to kill members of the enemy groups while minimizing the risk to attackers, and surprise helps to achieve this lopsided result. In other words, offense trumps defense. Successful raiders may also carry off resources such as food, animals, or women that will boost their own group's rate of reproduction and suppress population growth in the group they attacked.

In war, the odds of survival also strongly favor the victor. The asymmetry in casualty rates is most extreme for massacres, in which all or almost all of the losing group are killed. Among the Inuit, for example, ethnographic accounts document that the goal of warfare was annihilation of the enemy group (LeBlanc and Register, 2003, p. 118), and surprise dawn raids were the preferred tactic. Among tribal firming peoples, annihilation was also a typical goal in war, although men were the primary target and women might be integrated into the victor's society, which would take over the land of the defeated group. Even when the primary objective is winning rather than killing, losing increases casualties because people on the losing side tend to run away, presenting low-risk killing opportunities similar to those sought in surprise raids. Keegan (1976) notes that "the most dangerous course in war is to retreat when in close contact with the enemy . . . [which] appears to stimulate an almost uncontrollable urge to kill among those presented with a view of the enemy's backs" (p. 150). In summary, the selective pressures of war should favor any characteristic that promotes surprise attack and winning. Membership in a defeated group increases mortality, especially for males.

THE LOGIC OF MULTILEVEL SELECTION AND WAR

While individual behavior can certainly affect one's chances of survival in war, especially for those in the midst of a fight, the probability of being killed is also strongly influenced by what side one is on, winning or losing — in other words, on one's group membership. War kills not just individuals but members of groups. Hence evolutionary models of war should consider the possible role of group selection in addition to natural selection at the individual level.

Early group-selection models, which proposed an evolutionary advantage to groups that restricted population growth and hence did not degrade their resource
base (Wynne-Edwards, 1962), suffered from both logical and practical flaws. Williams (1966) pointed out that natural selection against individuals who restricted their own fertility would systematically weaken such tendencies over time. On a population level, members of groups that grow more rapidly will also become more common over time than those that restrict growth. For group selection to work (which Williams acknowledged was possible), the trait being selected cannot restrain reproductive success at the group level — instead, it must enhance it.

Sober and Wilson (1998) set out specific criteria for multilevel selection for group-benefiting altruism. In a population of groups in which the incidence of altruism varies, groups with a higher incidence of altruism must reproduce at a higher rate. The progeny of these groups must either mix with one another or otherwise compete in the formation of new groups. We followed these criteria in constructing our computational model, with war as the form of explicit competition that determines the composition of new groups. In multilevel models, whether group selection operates as a meaningful force depends on the relative strength of (1) natural selection acting on individuals within a group and (2) group selection operating on differences between groups. This logic, which requires that an individual's fitness be partitioned into within-group and between-group components, can be represented mathematically via a rearrangement of terms in Hamilton's equation for inclusive fitness (kin selection), which is widely accepted among evolutionary theorists (see Reeve, 2000, for the mathematical details). A similar reinterpretation of terms has been used to track the evolutionary accounting for reciprocal altruism, applied by Patton to war among Amazonian tribes (Patton, 2000).

THE EVOLUTION OF COMMUNITARIANISM AND HEROISM: A COMPUTATIONAL MODEL

Our model has the following general structure: A population of individuals is divided into several groups. Each group occupies a territory that provides resources for survival, and each group member has some propensity (between 0 and 1, representing never and always) toward what we call communitarianism — nonmilitary altruistic behavior that benefits in-group members (via acts such as food sharing or care of the injured or wounded) and that comes at a cost to one's own reproductive fitness. Communitarianism increases the overall growth rate of the group (baseline fertility) at some cost to the sharing and caring members, who might otherwise choose to hoard food stocks or let weaker group members die, removing in-group competitors for food and other resources.

When a group's population exceeds the carrying capacity of its natural resources, it attacks another group at random. The outcome of the attack is determined by the number of individuals who participate in fighting in each group and
by the propensity of each fighter for altruistic heroism. Heroism also ranges between 0 and 1, with 0 representing no participation in dangerous fighting/defense and 1 representing maximal heroism. Larger groups have an advantage, but a smaller group can plausibly win if its members are more heroic. Indeed, such victories by a smaller but heroically motivated force play an important role in collective mythology and history (for example, in the fourth act of Shakespeare's Henry V—"We few, we happy few, we band of brothers"). Once the outcome is determined, members of the losing group are annihilated (or otherwise vacate the territory and the simulation, perhaps becoming refugees), and the winning group fissions, with some members moving to the vacated territory.

At the end of each generation, each individual has some probability of reproducing, and offspring resemble their parents in communitarian and heroic propensities within a specified range of variation. In the current version of the model, our focus is on phenotypic behavior at the level of individuals and groups. Individuals who express these behaviors are the unit or object of natural selection, while what is selected for is the behavioral propensity (see Mayr, 2001, pp. 126–134, for a good discussion of objects of selection). We make the explicit assumption that behavioral tendencies are heritable, consistent with evidence from behavioral genetics (Loehlin, Willerman, and Hom, 1988), but genes per se are not modeled, and we do not presume that there is a particular gene for heroism or for any other complex social behavior. We do assume that offspring resemble their parents. The range of variation stands in for the more explicit genetic mixing of sexual reproduction and for the imperfect association of genotype and phenotype. In human societies, of course, broader cultural structures can reinforce or dampen the expression of any behavioral tendency, but we do not include culture in the current model, only direct transmission from parent to offspring. An individual's probability of offspring (reproductive success) is reduced both by communitarianism and (in the event of war) by heroism. In our model, the only cause of death is war.

By treating communitarianism and heroism as distinct sets of behaviors, we can investigate them separately as propensities that might plausibly have been selected by war but might also have developed in response to different sets of selective pressures. The model allows for individuals to be all-around citizens who are equally willing (or unwilling) to make sacrifices for the group in peace or war. It also allows for communitarian pacifists or heroic fighters who are not otherwise prone to peaceful altruistic acts.

The following parameters can be varied: number of groups, richness of natural resources in each group's territory (which effectively limits group size), baseline individual fertility (probability of offspring), extent to which communitarianism can improve fertility rates within a group, reproductive costs to individuals of communitarianism and heroism, number of generations, and mutation rate. For technical details including equations, see appendix 5.A.
To examine the selective pressure of war on communitarianism and heroism, we started by exploring the impact of two parameters: the maximum sustainable size of groups (which is constrained by the habitat resource base) and the relative costs and benefits of the two types of behavior. We chose group size to explore whether it has an impact separate from the proposed psychological effects often evoked to explain the robust finding that incidence and severity of social loafing and freeriding (selfish behaviors that damage group performance) increase in larger groups (for example, Latané, Williams, and Harkins, 1979; Seijts and Latham, 2000). The phenomenon has been attributed to the increasing difficulty of monitoring others' contributions and the corresponding decreased accountability of each member, coupled with a decreasing sense that one's contributions are critical (Kerr and Bruun, 1983). In our simulation, agents are unaffected by any feelings of responsibility or criticality—they simply act in accordance with their traitlike “propensities.” The model allows us to investigate whether, absent these psychological effects, the evolution of such behavioral propensities could still be affected by differences in criticality for heroism and the dilution of benefits of communitarian action based on group size.

We chose a range of group sizes consistent with ethnographic and archaeological literature that suggests that the size of hunter/gatherer bands would be roughly 20–50 people (Caporael and Baron 1997; Dunbar, 1993), increasing to around 100–200 for “cultural lineage groups” and Neolithic villages (Dunbar, 1993). Applying three additional assumptions—that warriors are male, that they are adults, and that there are roughly equal numbers of males and females in each group—we used the age demographics given for a few contemporary hunter/gatherer peoples (Hill and Hurtado, 1991; Howell, 1979) to give a rough estimate that around 35 percent of a group would be in the right age and sex categories to be warriors. This yields numbers of eligible warriors from a minimum of 7 for groups of size 20 to a maximum of 70 for groups of size 200. Because, in our simulation, all members fight (and hence we are, in effect, modeling the warrior segment of groups), the group sizes we chose for our simulation were 10, 25, 50, and 75. We kept the number of groups fixed at four, and all four habitats had equal carrying capacities (either 10, 25, 50, or 75).

We varied the cost/benefit settings to explore the relative sensitivity of the two forms of altruistic behavior to costs and benefits and also to identify the range in which multilevel selection would actually occur. The logic of multilevel selection requires that the forces favoring groups that benefit from altruistic behavior over groups that do not are at least as strong as the selective forces favoring selfishness among individuals within groups. However, for both heroism and communitarianism,
some of the benefits are affected by emergent properties of groups and wars and hence are not directly controlled by parameter choice. The benefits of war depend on winning, and winning depends on a combination of relative group size and heroism. The benefits of communitarianism that redound to an individual group member are also affected by the number of individuals contributing and by whether group size proves to be pivotal in particular wars. Since these are emergent factors, we could not directly calculate a priori when costs at the individual level would be balanced by benefits at the group level.

Focusing on the costs and benefits that are determined directly by parameter settings, we chose three cost/benefit levels for the experiment: a low-cost, high-benefit setting; a high-cost, low-benefit setting; and an intermediate setting. We subsequently refer to these as the low-, high-, and medium-cost conditions. The benefit was implemented as the maximum increase in group-level reproductive rate (probability of offspring) that could be achieved if all members of a group were 100 percent communitarian. The cost was how much communitarianism and heroism affects reproductive success (assuming survival to the reproductive phase). To facilitate direct comparisons, the cost of heroism and the cost of communitarianism were the same for each condition (for more details, see appendix 5.A). The two factors were crossed, and 10 runs of 2,000 generations each were completed for each of the 12 cells, for a total $n$ of 120. Initial mean values of both communitarianism and heroism were .5 for all groups, a choice that allows for observation of both increases and decreases over time.

RESULTS

As expected, both communitarianism and heroism were sensitive to cost, evolving to higher levels when the cost/benefit setting was more favorable. However, communitarianism was more sensitive to cost than heroism and evolved to mean levels above the starting point of .5 only at the low-cost setting or when the sustainable group size was small (10 or 25) and the cost was moderate. Figure 5.1 shows the mean communitarianism values for the final 500 generations of the 2,000-generation runs for the 12 conditions. Heroism, in contrast, evolved to higher levels than the starting value under all conditions (Figure 5.2). The number of wars was clearly sensitive to the cost/benefit setting (Figure 5.3), which sets a limit on maximum baseline group fertility. The decrease in war frequency with larger group size for the low-cost and medium-cost conditions tracks the pattern for communitarianism, which makes sense given that mean group communitarianism is what increases fertility. When communitarianism is relatively "cheap" and yields substantial benefits to group fertility, population growth leads groups to outstrip the carrying capacity of their territories more quickly, triggering frequent wars (about one and a half per generation under the low-cost condition, which translates to a 75 percent likelihood of each group being in a war each generation).
Figure 5.1
Evolved Communitarianism for Different Cost and Size Settings: 120 Runs of 2,000 Generations Each (10 runs per cell)

Figure 5.2
Evolved Heroism for Different Cost and Size Settings: 120 Runs of 2,000 Generations Each (10 runs per cell)
Heroism, in contrast, neither triggers nor requires frequent wars to evolve. Even in the high-cost, larger-group-size conditions in which communitarianism collapses and groups experience war on average only about once every six generations, heroism can still evolve to quite high levels. Although this might at first seem counterintuitive, since heroism only yields benefits during war, the cost of heroism is also paid per war rather than per generation. This makes sense because only in war does heroism expose a warrior to danger. In peacetime the behavior is not expressed, within-group natural selection against heroism does not operate, and any changes in heroism are simply genetic drift.

The relationship between number of wars and communitarianism (both emergent properties in the simulation) is bidirectional: While wars, fission, and migration provide a group-level selection mechanism for communitarianism in line with the logic of Sober and Wilson (1988), the resulting increase in fertility also promotes overpopulation, triggering wars. In our model, multilevel selection for communitarianism via warfare gains traction in an environment of runaway population growth and persistent intergroup violence. The evolution of heroism based on war is more robust, and a relatively small number of wars selects for heroism almost as strongly as do constant battles.
To test the statistical reliability of the patterns just described, two-factor analyses of variance (low, medium, and high cost crossed with maximum sustainable group size of 10, 25, 50, and 75) were conducted to investigate the impact of these predictors on the evolved values of communitarianism and heroism. For communitarianism, size, $F(3, 108) = 25.46$, cost $F(2, 108) = 74.35$, and the cost by size interaction $F(6, 108) = 6.34$, were all significant at the $p < .001$ level, with an adjusted $R^2$ of 0.68 for the model. The nature of the interaction is evident in Figure 5.1: The evolved level of communitarianism is more affected by group size when costs are medium or high than when costs are low. For heroism, size and cost had significant main effects, $F(3, 108) = 3.58, p < .02$, and $F(2, 108) = 10.59, p < .001$, respectively. The cost by size interaction term was nonsignificant, $F < 1$, with adjusted $R^2$ of 0.18 for the model.

Because of the impact of communitarianism on war via fertility and unsustainable population growth, the outcome variable for communitarianism (mean for the last 500 of the 2,000 generations) was entered as a covariate in a factorial analysis of covariance (ANCOVA) predicting the total number of wars from maximum sustainable group size and cost. As expected, the covariate accounted for a substantial amount of variance, $F(1, 107) = 63.98, p < .001$. Cost, $F(2, 107) = 149.21$, and the cost by size interaction term, $F(6, 107) = 4.64$, were significant at the $p < .001$ level, Size was nonsignificant ($F < 1$), and adjusted $R^2$ was 0.92 for the model.

Beneath the orderly pattern of means for the last 500 generations evident in Figures 5.1 and 5.2, substantial variability was apparent among the trajectories across time for multiple runs in many of the 12 conditions covered in the design. Fortunately, analyses of variance are robust against violations of the homoscedasticity assumption with the equal cell sizes provided by our design (Hays, 1988). This variation is not just a nuisance; it is interesting in its own right, showing the extent to which trajectories of evolution are consistent and predictable given a fixed starting point and specified group size and cost/benefit parameter values.

Figures 5.4a–5.4c illustrate some differences. With high cost and large group sizes, the evolution of communitarianism follows a consistent trajectory of sharp decline and persistently low values (Figure 5.4a). With medium cost and a sustainable group size of 25, however, considerably more variety is evident (Figure 5.4b). Although a dominant trajectory is apparent, with 6 of the 10 runs showing a steady increase ending at values between .8 and 1.0, one of the runs follows the trajectory of immediate decline we saw in Figure 5.4a, another decreases to low levels but recovers and ends up the same place as the steadily increasing trajectories, and the other two trajectories are eccentric and unstable, rising to high levels only to collapse precipitously. For high cost and sustainable group size of 10 (Figure 5.4c) all predictability vanishes; although all the runs start at the same initial value and unfold in identical environments as defined by simulation parameters, ending values span the full range of possibilities, and there is no central tendency. The three figures together illustrate a
Figure 5.4
Communitarianism for Individual Runs across 2,000 Generations for Three Parameter Settings: (a) High Cost, Sustainable Group Size of 75; (b) Medium Cost, Sustainable Group Size of 25; (c) High Cost, Sustainable Group Size of 10*

* Each group shows 10 runs with identical parameter settings. Sustainable group size is based on the fixed size of a group's resource base. See appendix 5.A for simulation details.
lesson common to studies of complex systems, which is that changes in control parameters can change not only the mean values of state (outcome) variables, but the degree of predictability in the system, from the inevitable result of a single strong attractor to the unpredictability of rapidly diverging trajectories (Arrow, 2005).

**DISCUSSION**

**Group-Serving Behaviors in Intragroup and Intergroup Contexts**

Our theorizing, as implemented in our computational model, suggests that a propensity for heroism—a human impulse to risk injury or death to protect, defend, and do battle on behalf of one's group—could have evolved in a setting in which heroism helped groups win wars, even if more heroic group members risked dying without issue and even if genocidal conflicts were relatively rare. Other forms of selection that deliver hidden benefits for such behavior—whether via reciprocal altruism (Patton, 2000), sexual selection (Miller, 2000), or kin selection—have likely contributed to stabilizing and reinforcing these tendencies. As Tooby and Cosmides (1996) propose in analyzing the evolution of friendship, once useful adaptations develop for delivering benefits to others, further evolution tends to reduce the costs and create compensations that make the delivery of benefits rewarding. Another contributing factor could be the Baldwin effect, whereby beneficial behaviors that are originally not tied to genes are reinforced by the selection of genetic determinants for such behavior (Mayr, 2001, p. 137).

In contrast to the robust results for heroism, warfare in our model only selected for intragroup communitarian tendencies under extreme conditions of perpetual war, high benefits to group fertility, and low costs to individuals. Inconsistent and variable results across multiple runs also leads us to believe that group selection for such behavior via warfare is quite unlikely to have occurred. This does not preclude selection for apparently self-sacrificing intragroup behavior by other mechanisms, of course, but it does suggest that pushing the intergroup conflict button should trigger a stronger and more reliable response than pushing the good-of-the-group button when there is no perception of threat from another group.

Anecdotal evidence that group-serving behavior is easier to evoke in the context of intergroup threat is abundant: The power of the “rally 'round the flag” effect provides a ready temptation for political leaders to evoke out-group enemies as a unifying strategy. Empirical results from studies using intergroup social dilemma paradigms also indicate that when a mixed-motive game is embedded in an intergroup context, people are less likely to free-ride (Bornstein, 1992), although the pattern of increased intragroup cooperation appears more reliably for males (Van Vugt, De Cremer, and Yuki, 2006). (Other studies have also shown different patterns of in-group favoring choices for men and women—for example, Gaertner and Insks, 2000.) The widespread use of war rhetoric as a strategy to inspire collective effort in endeavors as inconsistent with war as medical research (war on
cancer) and economic development (war on poverty) may also express an implicit understanding that the prospect of war is more invigorating than the prospect of peace.

**Size and Cost Constraints: When Is Self-Sacrificing Behavior Worth the Price?**

Many explanations for apparently altruistic behavior show how, at a different level of analysis (typically the gene instead of the organism), the behavior is ultimately beneficial. In fact, this must ultimately be true (on average) for any costly phenotypic characteristic to be selected. The sensitivity of evolved communitarianism to group size and to relative costs and benefits suggests a similar explanation. Although an upstanding communitarian will be at a disadvantage relative to fellow group members who are less devoted to the group, the increase in baseline fertility due to one's own actions could be enough to provide a reproductive advantage compared with the whole population of humans, as long as other groups benefited from less communitarianism overall and hence reproduced at a slower rate. Because the increase in baseline group fertility in our model is based on the average communitarianism in the group, the relative impact of one's own actions is greater the smaller the group.

The same logic holds for heroism, but to an even greater extent, given the admittedly extreme assumption that all members of the losing group die (complete genocide). If one's own actions are critical to victory, then escaping certain death in defeat should be a powerful incentive regardless of any group-serving motivation, and the likelihood of proving critical should be inversely related to group size. Using a formal mathematical model that varied the genocide parameter and assumed that people were either complete heroes or utter cowards, Smirnov, Arrow, Kennett, and Orbell (2006) demonstrated that an equilibrium population frequency does exist at which the expected value of being heroic or cowardly is the same and the expected frequency of heroes also declined.

If the ultimate average fitness (reproductive success) for those who engage in communitarian or heroic behavior exceeds the average fitness for groups in which few people are heroic or communitarian, does their heroism or communitarianism still count as altruism? Yes and no. The answer is yes from the perspective of the in-group that benefits from the behavior, but no for the broader context, including others whom the person only encounters in war and who decidedly do not benefit from (in fact, are harmed by) the same "altruistic" actions. The discrepancy between the two ways of calculating benefit have implications for evolved psychological mechanisms promoting such behavior. We explain why in the following section, which widens the scope from our particular model's results to speculate on
the likely consequences of war as a selective pressure on human cognitive and behavioral evolution.

**Implications for the Conflict in and between Groups in the Twenty-First Century**

Most people, most of the time, are thankfully not engaged in open warfare in the twenty-first century. However, we do continue to live and work in group settings, and whatever shaping of human cognition and behavior that war has wrought is still with us, part of the motivational complex (Gat, 2000) that selects from among a complex repertoire of potential actions. In this section, we go beyond the simulation results to suggest some implications the psychology of war might offer in understanding intergroup and intragroup behavior. For this discussion, we draw broadly on both psychological literature and other material on war.

One reader of an earlier draft of this chapter suggested that opening with the example of emergent warfare on an isolated Polynesian island was inappropriate for an essay "about war in the Pleistocene." We kept the opening because it helps signal that we are not just interested in war in the remote past; we are also interested in how human beings in general behave in groups. We believe that the consequences of selective pressures exerted by war might help us understand not only why the population of an isolated island fragmented and retreated into hilltop fortifications sometime in the fifteenth or sixteenth century (Kennett, Anderson, Prebble, Conte, and Southon, 2006), but also why members of work groups in a Fortune 500 company tend to polarize along faultlines, increasing conflict and damaging group performance and member satisfaction (see chapter 3 in this volume).

In this section, we propose some propensities that might function as adaptations to war. We also suggest some implications of those propensities for understanding conflict more generally.

**Irrational Enthusiasm for War**

As we mentioned in the introduction, a form of cultural selection known as equilibrium selection can occur when groups with a culture that promotes group-serving behavior outcompete groups that lack such reward systems (Boyd and Richerson, 1990). Behavior aimed at securing rewards specified by the culture requires little explanation, and clearly many societies actively promote and reward behaviors that, absent such rewards, would be counted as altruistic. For example, if serving in the army was expected to pose a small threat of actual danger and was rewarded handsomely with huge salaries and high societal prestige, it would surprise no one if many people actively sought to enlist. What is harder to understand is why people would
flock to recruiting stations when the expected costs of joining the army sharply increase, as they do when a country is openly preparing for war. The logic of multi-level selection may provide a partial answer.

When the average global payoff for actions (assessed across the whole population) is positive but appears to be suboptimal when assessed locally, then rational calculations based on local information will dissuade people from action that may be ultimately beneficial. Cultural reward systems can help to tilt the scales, but getting people to embrace behavior that does not appear to be in their own self-interest should continue to be a hard sell. A motivational system capable of promoting such actions in the absence or insufficiency of culturally determined rewards will therefore need to disable the tendency to rely on rational cost/benefit analyses.

We believe this may help explain how the notable tendency of people to disregard the seemingly obvious dangers of war and get caught up in irrational enthusiasm for military adventures could have developed. LeShan (2002) documents both the human attraction to war and the profoundly unrealistic convictions (he calls this "mythic reality") that take hold of people as a group or society transitions from peacetime to wartime. If groups that included people invigorated by the prospect of bloody battles outcompeted groups that did not, such "irrational" enthusiasms would ultimately be an asset. As Montesquieu (quoted in LeShan, 2002, p. 33) noted, "A rational army would run away," but running away is a sure path to defeat and likely slaughter. Hence, we expect that at least some of the cognitive and behavioral propensities selected by war will prove difficult to square with rational calculations.

How is this relevant to teams in organizations? Once an intergroup conflict is openly labeled as war or develops features that prompt a group to interpret the situation as war, attempts to reason with the parties involved should have little or no effect. This is analogous to the disabling of rational thought that occurs when individuals become highly emotionally aroused—for example, when they are in the grip of panic or rage. In the case of an individual, the most pressing first step is to get the person involved calmed down so he or she is capable of processing information more systematically. Similarly, members of groups who have shifted to a mythic mentality need to be shifted out of that mentality to regain their connection to ordinary sensory reality.

LeShan (2002) suggests that stress and uncertainty increase the tendency to shift to mythic reality and that once the shift is made, the satisfying experience of bonding with the in-group provides a powerful reward. Members of a group that have bonded in the crucible of intense intergroup conflict are likely to discount or ignore anticipated negative outcomes for the group, as evidenced by the tenacity of German fighting units that kept up their resistance in World War II long after eventual defeat had become a virtual certainty. As reported by Shils and Janowitz (1948), the most powerful countervailing force in these strongly bonded units was a soldier's
concern for a different primary group—his family. Redirecting group members’ attention to other important relationships that might be damaged by the conflict is thus one strategy for spilling wind out of the intergroup conflict’s sails. In intractable cases, another solution is to break up the groups involved and reassign people to different units.

Results from a study using the intergroup prisoner’s dilemma (IPD) game showed that when people were able to communicate with other in-group members (the typical situation for any team that deserves the name), participants tended to increase their contributions to the group even when this resulted in a worse outcome for everyone—including self, in-group, and out-group. The structure of the game models unhelpful contributions that divert a group away from productive activity and toward intergroup hostility. When intragroup communication was not permitted, people decreased their contributions and achieved the outcome that was best for everyone (Goren and Bornstein, 2000). Separated from their groups, members resort to being individuals again and focus primarily on their own outcomes.

RAISE THE BARRICADES AND CONTAIN THE EMPATHY RESPONSE

Along with the reduced capacity to reason realistically about the conflict, another mechanism that is adjusted in a war situation is a general concern for other human beings. Caring stops abruptly at the in-group boundary. War, unlike peaceful interactions such as trade, does not require the mutual consent of both groups. Any group that lacks members willing to defend the group, with force if necessary, is at a disadvantage. Despite the ample historical evidence that people are quite capable of killing one another, often with disturbing enthusiasm, Grossman (1995) argues that the majority of humans are, like most other mammals, disinclined to kill conspecifics. According to Grossman (1995), soldiers must overcome or disable a natural and intense resistance to killing other human beings. Cognitive strategies and strong emotions triggered by war that help remove this "safety catch should convey a military advantage. A clear boundary between us and them helps. Consistent with Grossman’s perspective, and in line with the extreme moral convictions evoked by the transition to mythic reality, Ernest Becker (1975) asserts that “[m]ost men will not usually kill unless it is under the banner of some kind of fight against evil.” The proper response to people defined as evil is not a caring response, but denunciation and attack. Because impulses are cheaper than action, we would expect to see violent emotions expressed toward enemies to be more common than violent action.

If war operates as an agent of group selection, it kills people not because of any individuating characteristics they possess, but simply because of their group membership. Hence cues that trigger war-related schemas should heighten attention to group
identity and group boundaries. Evidence from experiments using the minimal group paradigm (Brewer, 1979; Tajfel, Billig, Bundy, and Flament, 1971) show how easy it is to evoke such attention, even in the absence of threat and when group membership is based on obviously trivial criteria.

Reclassifying out-group members as nonhuman and therefore not covered by the prohibition against killing could be functional in this way. Social-identity theorists explain in-group favoritism and out-group derogation as strategies to help one feel good about oneself (for example, Brewer, 1979). However, this explanation does not account for the practical function of such identity enhancement or suggest why people would abruptly experience a sharply increased need for self-enhancement in wartime. Terror management theory (TMT) (Greenberg, Solomon, and Pyszczynski, 1997) does a somewhat better job, suggesting that enhancement of self-esteem and the need to counter threats to the in-group's cultural worldview are driven by defensive motives: They protect us from "deeply rooted fears concerning our vulnerability and mortality" (p. 11). Oddly, however, given the explicit attempt to ground TMT in evolutionary thinking, the eponymous terror of the theory is existential, brought on not by any real-life threat, but by the paralyzing but ultimately abstract knowledge that we are mortal. We agree that the management of terror has an adaptive function, but we suggest that the terror that most needs to be managed is that evoked by the real or imagined threat of brutal violence against self and kin. From an evolutionary point of view, mechanisms that help protect one from death are more likely to evolve than mechanisms that help protect one from unwanted thoughts of death.

Bonding and heightened empathy for one's in-group, coupled with a sharply reduced concern for denigrated others outside the group boundary, should help frightened people overcome the "freeze response" and effectively counter the threat. A motivational system that rewards us for affirming the value of in-group culture and derogating out-group members, especially when cues indicate a war environment, can clear the way for the unpleasant but functional business of committing violence against fellow human beings.

In a context of enhanced group boundaries evoked by threat, any indicator of divided or suspect loyalties among fellow in-group members should immediately attract attention as a possible danger signal. For most of human evolution, groups did not gallop or sail or fly long distances to fight distant enemies; they fought with their neighbors, the same people they also interacted with in nonviolent ways by trading mates and goods. As LeBlanc and Register (2003) note, "Planning a massacre treacherously disguised as a feast or celebration is an example of such shifting behaviors and is a recurrent theme around the world" (p. 68). If this strategy, like the surprise dawn raid, was a common feature of early human warfare, then paranoia and suspicion of treachery could be selected for as protective mechanisms that might save one's group from disaster.
The tightening of group boundaries in response to intergroup suspicion suggests a potential extension of TMT beyond free-floating anxiety about one's own death. Terror management theory proposes that threats to one’s cultural worldview endanger the psychological defense mechanisms constructed to keep existential dread at bay. The self is viewed as individual, isolated. However, if one focuses on the relational or collective self, threats to the group might be the more motivating danger, and intragroup conflict is one of those threats. Worchel’s (1994) cyclical theory of group development identifies the period of decay as a time when members pay increasing attention to personal needs and when intragroup conflict and competition increase. Subgroups may form and compete for power, and disaffected members may defect to other groups as the group drifts into discontent, with most members feeling helpless to influence the group. To rescue the group from the danger of disintegration, a precipitating event is called for. Worchel (1994, p. 211) notes that “the incident may be relatively minor and unplanned, such as the rumor of mistreatment of a group member, or it may be more dramatic (a riot), and in some cases staged. In small groups, the incident may be an emotional outburst or attack by a single member.” If members become anxious about the survival of the group, directing attention to a real or imagined external threat could trigger increased vigilance about defending the group culture and worldview and could spark renewed commitment and group identification. Projection of conflict outward could be functionally effective in repairing intragroup dynamics.

A Rumor of War

In our computational model, the path to war leads from overpopulation to resource scarcity, consistent with materialist theories of war (for example, Harris, 1984; Ferguson, 2000). We view this as a simplifying assumption in line with work that finds an association between resource stress and war, not as endorsement of a particular theory about one cause of war being necessarily more important than another. We do expect a perception of resource scarcity and associated suspicions that another group might threaten an important in-group resource to trigger war-adapted responses, both functional (pull the group together) and not so functional.

In his study of deadly ethnic riots, which fit our broad definition of war as coalitional violence, Horowitz (2001) found a consistent pattern of rumors that preceded deadly riots. One common theme was that the target group was planning to poison the in-group's food or water. In an atmosphere of anxiety, rumors circulated quickly and became more exaggerated, and no evidence was required for the rumor to take hold. Another common rumor was that the target group was planning an attack or that one or more members of the in-group had already been attacked. (Again, no evidence whatsoever was required for the rumor to be believed.)
In organizational contexts, analogous rumors of resource threat and impending attack can trigger intergroup war schemas. At the organizational level, the prospect of a merger or disputes between management and labor could prove to be a fertile setting for rumors of mass layoffs, for example, which are analogous to threats of annihilation by an outgroup. At the level of the work group, rumors and suspicions by subgroup members on either side of a faultline could trigger a reframing of group interaction as involving hostile intergroup rather than conflictual intragroup or interpersonal relations.

**Faultlines and the Identification Mechanism**

When intense conflicts develop in organizations (in which people often belong to multiple groups) or within a group, which group or subgroup will they turn to as their primary in-group? If a conflict starts to split a larger group in two, how will people line up? The psychology of war provides some relevant theory.

Shaw and Wong (1989) propose that war and evolution have shaped an identification mechanism that directs people's attention to particular markers that signal shared membership in a kin group. These markers, they propose, guide people to identify with particular groups in a war situation. The markers are common language, shared phenotypic characteristics, common religion, shared homeland, and belief in a common descent.

Shaw and Wong's (1989) emphasis on the importance of kin markers suggests a testable hypothesis for the relative impact of faultlines (Lau and Murnighan, 1998): More severe and disruptive conflict among subgroups should develop when the faultlines match more of the markers that signal shared membership in a kin group. Faultlines based on characteristics such as age, gender, or status (which routinely vary among close kin) should have a less powerful impact than faultlines based on language, religion, or belief in a common descent. Phenotypic similarity is a more questionable category, based on the finding that attention to visible differences that signal coalition membership (for example, the color of a sports uniform) can dramatically reduce the tendency to notice and encode more stable phenotypic features such as skin color (Cosmides, Tooby, and Kurzban, 2003).

**The Best Defense and Winning at All Costs**

Horowitz noted that although initial rumors of impending attack or atrocities are often unfounded, they provide a reliable predictor of what the threatened group will do once it launches its own, typically "preemptive," attack. Recall that in the surprise raid or ambush, which is likely the most ancient (and still a highly effective) war tactic, the advantage is with the attacker. If behavioral propensities related to intergroup conflict are sufficiently integrated that they tend to be coactivated, the motivations
triggered by intergroup schemas should include not only defensive solidarity but also the impulse to attack. Certainly this was true of the two groups of boys (the Rattlers and the Eagles) who participated in an early study of intergroup relations conducted at Robbers Cave State Park in Oklahoma (Sherif et al., 1961). When the presence of another group was announced, "the Rattlers immediately wanted to challenge them, and to be the first to challenge" (Sherif et al., 1961, p. 94, emphasis in original). One Eagles member issued a challenge to the Rattlers through the staff (p. 95) before having actually met any of the other campers.

Just as means must be found to disable any sympathy for out-group members, the immoral nature of an unprovoked attack must be somehow justified. This suggests an alternate interpretation of the rumors that precede an attack. Rather than viewing these as a cause of hostilities, Horowitz (2001) suggests that the inflammatory rumors are a projection of hostile intent on the chosen target that helps rally people to the cause and justify the forthcoming attack in the guise of defense.

Unlike social identity and in-group favoritism, analysis of attack motives is not a prominent theme in the social psychological literature. A study in the TMT tradition does provide potentially relevant findings on the acceptability of unprovoked attacks in the form of hate crimes against out-group members. Participants primed to have high mortality salience by answering questions about their own death were less punitive toward hate crime perpetrators (who were clearly attacking a member of a stigmatized group) than were participants in a control condition who answer questions about dental pain (Lieberman, Arndt, Personius, and Cook, 2001). If we reinterpret the mortality salience manipulation as a cue associated with wartime conditions (in which there is a real and present danger of death), then a more lenient view of unprovoked attacks (consistent with militarily advantageous surprise attacks and raids) would make sense.

Whether a group is in the role of attacker or defender, the single most important protection against the threat of death in war is to be on the winning side. Hence, when wartime schemas are activated, a strong motivation to win at any cost may well have developed as an adaptation promoting survival via the survival of one's group. Despite historical efforts to "tame" war and make it more civilized and less lethal, the desire to win creates a constant temptation to break the rules, commit war crimes, and violate agreements to refrain, for example, from strategic bombing of civilian populations. "Total war" represents the ultimate implementation of the motivation to win at any cost. The endorsement of this strategy in team sports, the source of the famous quote "Winning isn't everything, it's the only thing" (usually attributed to Vince Lombardi, but originally coined by UCLA football coach Henry "Red" Sanders in the 1930s [Overman, 1999]), connects war and sports thematically as settings for intergroup conflict—the first lethal, the second tamed (like ritualized battle or dominance contests) to reduce or eliminate mortality.
Many veterans who are honest with themselves will admit, I believe, that the experiences of communal effort in battle even under the altered conditions of modern war have been a high point in their lives . . . which they would not want to have missed.

The thematic connection between war and sports provides a useful thread to tie together the functional and dysfunctional ways in which the legacy of war may have shaped the human tendency to resolve conflicts of interest in favor of the group. An atmosphere of threat can evoke inspiring acts of group-serving behavior (heroism) that provide an example for others and get members working effectively together. According to Alexander's (1979) balance-of-power theory, the predatory threat of other human groups and the need to combine forces with other small kin groups to create a balance of power provided the necessary and sufficient forces for the emergence of forms of group living and higher-level organization that are the basis of all of our social and economic institutions today. "I am not implying," Alexander clarifies, that no other forces influence group sizes and structures, but that balances of power provide the basic sizes and kinds of groups upon which secondary forces like resource distribution, population densities, agricultural and technological developments, and effects of diseases exert their influences. And I am suggesting that all other adaptations associated with group-living, such as cooperation in agriculture, fishing, or industry, are secondary—that is, that they are responses to group-living and neither its primary causes nor sufficient to maintain it, at least in a world not so densely crowded with humans that there is essentially no way to live alone. (Alexander, 1979, pp. 222–223)

A balance of power may also be the key to taming warlike responses and channeling them into rule-based systems of intergroup engagement, so that groups that have retreated to hilltop fortresses in fear can be coaxed down from the hills to engage in invigorating but nonlethal contests in the valleys. If the rules of competition are kept fair and standards of behavior are rigorously enforced to prevent a reversion to the more vicious forms of conflict natural to war in the wild, the potential of intergroup conflict to enhance both performance and satisfaction within groups is substantial. Recent reviews of the intragroup conflict literature (e.g., De Dreu and Weingart, 2003) provide a sobering view of intragroup conflict as having systematically negative effects on group performance and member satisfaction. Intergroup conflict can provide a powerful—but dangerous—medicine for these ills.
The theory of optimal distinctiveness (Brewer, 1991) suggests that the fundamental tension humans must negotiate in groups is to find the right balance of connection and distinctiveness. LeShan (2002) suggests that there are two ways of providing a profound and deeply satisfying resolution of this tension. The first is meditation. The second is "the way of armed group conflict" (p. 28). As LeShan notes, "What war promises differs from what it delivers." But its enduring attraction for humans, including those with experience of its worst horrors, has not been extinguished, partly because of how well it delivers in terms of a profound group experience. The problems posed by war remain unsolved, but domesticated forms of this powerfully motivating social activity, played out in the more controlled environment of organizations and work groups, may yield at least a strong echo of the intense satisfaction and peak group performance that war evokes.

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Appendix 5.A: Details of the Formal Model and Explanation of Settings for Different Factor Levels

The world in the simulation consists of several territories with fixed boundaries. A territory $g = 1, 2, \ldots$ is endowed with $R_g$ natural resources. A number of individuals who populate this territory, $n_g$, form a group consuming its resources. Survival of the group's members is secured if resources per capita do not fall below an exogenous survival threshold, $T$: $R_g/n_g > T$; otherwise, the group attacks another group.

In the simulation runs reported, the number of territories was fixed at four, and each of the four territories had the same level of natural resources, $R_g$, fixed at 10, 25, 50, or 75 for the four "sustainable group size" conditions. $T$ was fixed at 1.

Members of all groups have the same baseline fertility, $P_b \in [0,1]$, a natural probability of having offspring in a generation. Baseline fertility can be adjusted for each group depending on its members' average communitarianism. With the latter incorporated, the resulting baseline for the group $g$ becomes $P_b + P_c A_g$, where $P_c > 0$ is the fertility difference between purely communitarian and noncommunitarian groups, and

$$A_g = \frac{1}{n} \sum_{i=1}^{n} c_i$$

is the group's average communitarianism, with $c_i \in [0,1]$ being the propensity of member $i$ for this form of altruism. Individual communitarianism is costly to fertility, decreasing the probability of having an offspring by $\gamma < 0$; the cost (set exogenously) is assessed proportional to $c_i$. The cost was varied in the runs reported in the text as described below.

In all of the simulation runs reported, baseline fertility absent communitarianism ($P_b$) was set at 0.1. $P_c$ was varied by setting the maximum fertility for complete communitarianism (all members at the maximum level of 1) at .75 for the low-cost/high-benefit setting, at .5 for the medium-cost/medium-benefit setting, and at .25 for the high-cost/low-benefit setting. Cost was varied by setting $\gamma$ (the multiplier for reductions in fertility based on communitarianism) at .05 for low cost, .075 for medium cost, and .1 for high cost.

When population growth causes a group's resources per capita to fall below the survival threshold, that group attacks another group chosen at random. Groups must fight if attacked. Each member of a group can increase the group's fighting strength by altruistic actions in war—which we call heroism. Heroism is a continuous variable, $h_i \in [0,1]$. As with communitarianism, we assume that war fighting decreases the probability of having an offspring by $\gamma > 0$. The group with the greater fighting strength, defined as
wins. Members of the losing group die or otherwise vacate the territory; the winning group fissions, dividing its members between its original territory and the vacated territory so that resources per capita are equal in the two territories. Combining the factors above, the probability of member $i$ of a surviving group having an offspring is

$$P_n + P_c A_x - c_x h_y w$$

where $w = 0, 1, \ldots$ is the number of wars. Thus, within a single group, more communitarian individuals always have a lower probability of reproducing. The same is true for more heroic individuals if $w \neq 0$. However, groups whose members are more communitarian and heroic grow faster and are more likely to win wars. For the cost/benefit variations, we constrained $y$ to equal $x$ for all runs, making the cost of heroism and communitarianism equal. Because the benefits of heroism (increased probability of one's group winning a war) depend on the relative group sizes and heroism levels of other members for each encounter, it is emergent and endogenous, and hence not subject to experimental manipulation.

In each generation, an individual $i$ may reproduce depending on its probability of having an offspring. Reproduction is asexual and stochastic. Offspring attributes are copied from the parent subject to a uniform shock with zero mean and an exogenous variance (for all runs reported, the variance was set at .02), which represents the sort of variation that sexual reproduction generates—offspring tend to resemble each parent within a range of variability. In addition, with a very small exogenous probability (set at .001 for all runs reported), offspring attributes can be drawn from a uniform distribution $[0,1]$, which represents completely random mutation, in which an offspring's resulting trait value has no relation to the parent's value.