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As a Functionally Specific Form of Altruism.

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“Heroism” in Warfare

As a Functionally Specific Form of Altruism.

“When two tribes of primeval man, living in the same country, came into competition, the tribe including the greater number of courageous, sympathetic and faithful members…would without doubt succeed best and conquer the others.” Darwin, *The Descent of Man*, chapter 5, p. 156.

Abstract

The willingness of people to risk their lives fighting on behalf of their nation (which we call *heroism*) is a background assumption in the study of war, thus of international relations, but also an evolutionary puzzle. We use two computer simulations to explore the possibility that heroism could have evolved as a domain specific form of altruism, selected through humans' ancient past as a consequence of warfare. In the first, "altruism" is modeled as a generalized disposition that promotes both heroism and other, non-military, forms of group-benefiting behaviors—which we call *communitarianism*. In the second, heroism and communitarianism are modeled as domain specific dispositions free to evolve independently. Warfare promotes weak selection on generalized altruism, somewhat stronger selection on communitarianism, and substantial selection on heroism. Heroism evolves more readily when groups are small and relatively equal in size. However, the level of evolved heroism is unaffected by whether war is rare or common. An analytic model indicates that heroism should evolve to higher levels when the rate of casualties in defeated groups is high. Our results suggest why special purpose *modes* of altruism might evolve more readily than a generalized propensity for altruistic behavior.

When Homer asks in the Iliad “What god drove them to fight with such a fury?” he was posing a question that remains problematic three thousand years later: *What makes soldiers willing to fight at great personal risk for their polis, their tribe, their ethnic group, or their country?* There is no doubt that soldiers often do fight in this manner. In spectacular cases, of course, they have invited almost certain death by, for example, throwing themselves on grenades in order to save their comrades,[1] but the history of warfare is, in large part, the history of ordinary men (and, in recent times, women) who willingly confronted the risk of death when fighting for their tribe, country, or other group. In the present paper we call this behavior “heroism.” Heroism is well recognized as a potential human behavior, but the existence of heroism is most commonly treated as a background assumption in examining the nature of war. In this paper we address what we see as the central puzzle of heroism: How could it have evolved?

Most studies that address the puzzle of why people are willing to fight on behalf of a group have focused on “proximate” answers—emotional, cognitive or other mechanisms that prompt such behavior in the here and now. Thus, for example, loyalties to small groups of

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[1] Stories about such behavior are not apocryphal. According to Holmes (1985, p. 300), “Of the eight medals won by Marines on Peleliu in 1944, six were awarded to men who covered grenades with their bodies to save their comrades….” And, quoting a history of the US Marine Corps by Robert Moskin: “Five black Marines earned the Medal of Honor in Vietnam. All five were killed shielding their fellow Marines from exploding enemy grenades.” Not all who did this were actually killed; Holmes reports that two winners of the Medal of Honor in Korea survived having thrown themselves on grenades. Yet the *risk* of death from such action is, clearly, very high.

fighting comrades (Gat, 1999; Shills & Janowitz, 1948; Stern, 1995) or, perhaps, a regiment (Holmes, 1985), the rage and fear provoked by an attack, or threat of an attack, against one's own group (Horowitz, 2001), and cognitive errors such as overconfidence about the risks involved in heroism (D. D. P. Johnson, 2004; D. D. P. Johnson et al., 2006; Wrangham, 1999b) are all well known to support such behavior.

But this level of explanation is only part of the story, the other part being the "ultimate" or "evolutionary" processes that could have selected for such proximate mechanisms through evolutionary time. While most theorizing in the social sciences invokes only proximate mechanisms, those must have been put in place by some evolutionary process—perhaps selection on genes alone, perhaps on cultural patterns, perhaps on an interaction between genes and culture—meaning that a full explanation of the behavior in question should include both proximate *and* evolutionary processes. Here we focus on the ultimate, evolutionary question: *How could proximate mechanisms supporting "heroism" have been positively selected during humans' remote ancestral past?* Since, by definition, heroism involves a fitness cost to the individual (increased risk of death) but a benefit to other individuals in the group (greater chance of survival) we might expect it to be selected against, eventually disappearing from a population. Yet heroism certainly does happen with some frequency across all cultures, suggesting that it is a species typical trait. How could this be?

How altruism *in general* might evolve is, of course, a major question in evolutionary biology, and the several well-developed, classic answers seem likely to be part of the explanation for heroism more specifically. These include inclusive fitness or "kin selection" (Hamilton, 1964) which shows how altruistic dispositions can evolve through relatedness between the altruist and the recipient of an altruistic act,[2] and reciprocal altruism (Trivers, 1971), which shows how proximate mechanisms supporting "other benefiting" behavior can evolve via exchange relationships (see also Axelrod, 1984). More recently, theories of multi-level selection have been developed showing how altruistic dispositions can evolve as a consequence of the positive impact of altruistic behavior on group success and the subsequent schism of successful groups (most notably, Sober & Wilson, 1998). These models are not inconsistent with each other,[3] and each of them—separately or in conjunction with the others—could well be part of an explanation for heroism as one expression of an evolved, *generalized* disposition to altruism. In these terms, a general purpose altruistic disposition would be as likely to prompt heroism as it would be to prompt any other altruistic behavior.

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[2] Hamilton's rule is that altruism can evolve by this means under the condition $rb > c$, that is when the benefit to the recipient (b) multiplied by the relatedness of the recipient to the altruist (r) is greater than the cost (c) to the altruist. Inclusive fitness has been invoked by Alexander (1979) and also Shaw and Wong (1989) in their pioneering attempts to understand the genetic basis of humans' propensity to warfare. Importantly, none of these processes—or the possibility we will develop here—implies a mechanical or "deterministic" link between evolved cognitive mechanisms and behavior; as is well developed (e.g., by Geary, 2005; Marcus, 2004), such mechanisms characteristically operate on a contingent *If* (environment) *then* (emotion) basis, with behavior a product of complex interactions.

[3] Thus, Humphrey (1997) has argued persuasively that inclusive fitness and reciprocity "…have their roots in just one genetic trait: namely, a trait that is nothing else than *a trait for behaving altruistically to others who share this trait.*" (Italics in the original.) Similarly, inclusive fitness and reciprocity have been argued to be, in effect, multilevel selection models in their own right.

We develop the possibility that heroism could have evolved as a "domain specific" form of altruism in response to warfare in our ancestral past, rather than as an expression of a generalized propensity for altruistic behavior. The idea that human cognitive architecture consists, in substantial part, of functionally specific information processing modules is standard in evolutionary psychology and in cognitive neuroscience more broadly, and although differences exist between those arguing for a strong version of modularity (notably Cosmides & Tooby, 1994; Hirschfeld & Gelman, 1994; Sperber, 1994) and those seeing the possibility of at least some measure of domain generality (notably Buller, 2005; Fodor, 2000; Mithen, 1996), there is now a widespread acceptance that the human brain has a *substantially* domain specific architecture, incorporating multiple highly specialized information processing mechanisms. The standard argument for the evolution of strong modularity is given by Cosmides and Tooby (1994 p. 89) as follows:

> …different adaptive problems require different solutions… Speed, reliability, and efficiency can be engineered into specialized mechanisms because there is no need to engineer a compromise between competing task demands…As a rule, when two adaptive problems have solutions that are incompatible or simply different, a single general solution will be inferior to two specialized solutions.

The critics of this strong modularity position do not so much reject its basic logic as propose ways by which it must be qualified given the evidence for *some* selection on domain general mechanisms.

However this argument plays itself out, the extensive literature on altruism has, to our knowledge, focused exclusively on the problem of how a *generalized* disposition to altruistic behavior might have evolved and not on the possibility of domain specific altruistic dispositions having evolved independently, each in response to a distinctive adaptive problem, and each producing, therefore, at least somewhat different proximate mechanisms. Since heroism is, by definition, an altruistic response on behalf of one's group in the event of a violent conflict with some other group, its task demands would appear *prima facie* quite distinct from those of other altruisms (e.g., providing food and to others at some personal cost, caring for the sick)—meaning that heroism could have evolved on its own distinct trajectory and independently of such other forms.

Further, our interest is in the possibility that warfare itself has been the agent of selection in this case. Warfare is, by definition, a group-level phenomenon and, while its broad outcomes (victory, defeat, and standoff) are also group-level phenomena, these outcomes can have major consequences for the evolutionary success of the individuals comprising such groups. Most obviously, those who do the fighting in the group's wars run the risk of dying as a result, reducing the probability that their genes will pass on to the next generation, but all group members—those who fight as well as those who do not—can also suffer "genetic death" should the group be defeated. Conversely, should the group be victorious, those who survive stand to benefit significantly: Quite apart from males' sexual access to females from the defeated group (viz: rape, captured concubines etc.), the spoils of victory can include access to the defeated group's territory and whatever resources that territory contains. Clearly, frequent warfare during humans' ancestral past *could* have had major adaptive consequences—positive and negative—for individuals in the warring groups.[4] Since heroism as we have defined it is central to the outcome of wars, the evolution of heroism is a good candidate for being among those consequences.

How frequent *was* warfare in our ancestral past? Attempts to answer this question have provoked a good deal of controversy. Some accounts of the archeological record suggest that war was quite frequent. LeBlanc (2003, pp. xii - xiii), for example, comments:

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[4] A growing literature has addressed multi-level selection on normative systems and institutions, some of it paying particular attention to warfare as the agent of selection. Soltis, Boyd and Richerson (1995), for example, used the extensive ethnographic literature on New Guinea to assess whether warfare and associated group extinctions had been sufficiently frequent to account for the evolution of group-benefiting normative and institutional patterns, concluding that it had *not*; for such selective processes to have significantly influenced even one such group attribute, between 500 and 1000 years would have been necessary. Other work assessing the selective impact of warfare in multi-level terms includes Dawson (1999) and Richerson and Boyd (1998), and on multi-level selection more generally, see importantly Sober and Wilson (1998). Our interest is in selection as consequence of warfare on the *individual* attribute heroism, thus on genes (or, more realistically, on complex interactions among multiple genes) not on group-level attributes, such as normative systems or institutions. By comparison with selection on genes, cultural group selection can magnify phenotypic variation among groups while diminishing it within groups (Boyd & Richerson, 1985), meaning any finding that warfare selects for individual attributes will be conservative by comparison to what might be expected from cultural group selection, or any interaction between that and selection on genes.

> Just how common was warfare in the past? I have finally concluded that warfare was *quite* common in the past, and that my findings on three continents and within multiple time periods were not a fluke but the norm. This has led me to reason that if conflict *was* common, then it must have been an important occurrence in the course of human history. (Italics in the original.)

And with respect to the outcomes of warfare for the defeated populations, in a book that covers much the same territory as LeBlanc's, Keeley (1997, p. 93.) observes that the estimate of 100 million deaths from war-related causes in the 20th Century is

> …*twenty times smaller* than the losses that might have resulted if the world's population were still organized into bands, tribes, and chiefdoms. A typical tribal society lost about .5 percent of its population in combat each year. Applying this casualty rate to the earth's twentieth-century populations predicts more than 2 *billion* war deaths since 1900. (Italics in the original.)

Other authors have developed the same general theme (e.g., Carman & Harding, 1999; Martin & Frayer, 1997; Rice & LeBlanc, 2001), and Goodall's (1986) discovery that male chimpanzees sometimes engage in deadly raids and ambushes against neighboring populations raises the possibility that warfare among hominids may go back perhaps five or more million years, at least to our common ancestor with chimpanzees. (See also Alexander, 1979; Low, 1993; Wilson & Wrangham, 2003; Wrangham & Peterson, 1996).

There are, of course, qualifications. First, there were almost certainly times and places in which warfare was *not* "constant." To the extent that war was a consequence of group competition over adaptively important resources, we would expect very *little* warfare after humans colonized new areas. That appears to have been the case for a many generations after humans first migrated into the Americas (Hass, 1999, p. 14.; See also Wolf, 2001), and in East Polynesia warfare was similarly rare among founding populations—although it increased as populations grew and competition for resources mounted accordingly (Kennett, Anderson, Prebble, Conte, & Southon, In press; Kirch, 1984). The present analysis is based only on the possibility that warfare was *sufficiently* constant during our ancestral past to exert *some* selective pressure on heroism. We will return to just how constant warfare must have been for that to happen.

Second, disputes exist among anthropologists about the frequency of ancestral warfare under *any* demographic and resource-related circumstances. Fry (2006), for example, takes issue with authors such as LeBlanc and Keeley who, in his view, are simply expressing modern cultural beliefs about human nature being “essentially violent and warmongering” thus suggesting that war is as a result “natural,” and emphasizes as an alternative perspective “the human potential for peace.” (P. 2.) Whether Fry is correctly characterizing the position taken about human nature by these authors (and we think he is not), the empirical issue is the *incidence* of warfare in the ancestral past, not humans’ capacity for peaceful cooperation—which we think is obvious, being well developed across several disciplines—making Fry’s and related arguments (e.g., Fuentes, 2004; Sponsel, 1996) beside the point.

Happily, however, we do not have to referee any argument among anthropologists about the incidence of warfare in our remote, ancestral past. Few scholars dispute that warfare—or, more broadly, “coalitional violence”—has been present, at least to some extent, throughout that past, and the question here is whether warfare, happening with *any* significant frequency, could have selected for heroism. The simulations that we will now describe allow us to study the relationship between frequency of warfare and such selection, and we will report findings to that effect later in the paper.

Two Simulations

In the first simulation, *altruism* is domain general, performing two functions: (1) It promotes *communitarianism*—increasing the mean fitness of group members by group-benefiting behaviors that do not include fighting; and (2) it promotes *heroism*, contributing thereby to the group's success in warfare. In the second simulation, these two functions are performed by two independently evolving domain-specific attributes. A formal description of the two simulations can be found in Appendix 1; here we describe the key features of the simulations verbally.

Model 1: Domain general altruism

Groups and resources. Four groups each occupy a fixed resource base on which its members are critically dependent for nourishment. The size of the resource base for each group is a parameter; it may vary across groups but not across time and—because individuals must consume such resources in order for them to survive and reproduce—it sets a limit on sustainable group size.

Altruism. Each group member has a propensity to behave altruistically, which is modeled as a continuous variable with values between 0 (never) and 1 (always). The starting mean altruism of each group is a parameter of the model; the altruistic propensity of a group's members varies in a uniform distribution centered at the specified mean. An individual's altruism increases the reproductive success of all group members *and* contributes to the group's success in warfare as a function of that individual's particular altruism score (the more altruistic, the more benefit to others across both domains); the reproductive cost paid by the individual is similarly a function of that score (the more altruistic, the greater the cost to self).

Baseline Fertility and Individual Reproduction. Baseline fertility is the probability of each group member's having an offspring in a given generation—*prior to* any adjustments based on the incidence of altruism in the group (the more altruism summed across all group members, the greater each group member's probability of reproducing), the individual's own altruism score (the greater that score, the smaller the probability of that individual's reproducing), or the outcome of war (group members who do not survive wars do not reproduce). Should there be more than one war in a generation, the cost of participating (reduced probability of surviving to reproduce) is assessed separately for each.

Going to War. A group goes to war when its population exceeds the carrying capacity of the resource base—that is, when the resource base per capita drops below a specified threshold. At this point the only way in which a group can support its members is to capture the resources held by another group. Target groups are chosen at random from among the other groups, with any group that is attacked by another *having* to defend itself by fighting.

Particular wars, of course, often have highly visible proximate "triggering events" (the seduction of Helen, the assassination of the Archduke Ferdinand), but the visibility of such proximate events is not inconsistent with a more ultimate explanation in terms of population pressures on groups' resources (Shaw & Wong, 1989, p.11). There are doubtless causes of war other than scarce economic resources; Chagnon (1988) and others, for example, point to the frequency with which capturing females is the stated reason for hunter-gatherers going to war. It is also clear that tribes, societies, and nations do not necessarily go to war even if some or many of their members are starving. However, the idea that resource stress increases the *likelihood* of war (even if it does not serve as the direct trigger for war) is widely assumed among anthropologists, biologists, ethologists, political scientists, psychologists, sociologists and others addressing the ultimate causes of warfare (e.g., Alcock, 1978; Carneiro, 1970; Durham, 1976; Eibl-Eibesfeldt, 1979; Kennett et al., In press; Lambert, 1997; Lambert & Walker, 1991; Shaw & Wong, 1989; Thayer, 2004; van den Berghe, 1978; Wilson & Wrangham, 2003). David Geary (2005) makes the point succinctly:

> As our ancestors improved in their ability to secure resources from the ecology, the primary problem became staying in control of the best ecologies—that is, keeping other humans from securing the same ecological resources. (P. 7)

Warfare as a means for ensuring control over scarce resources is, of course, not unfamiliar in modern times, and it is the starting point of our model.

Victory and Defeat. The group with the highest summed altruism score wins. This represents the total amount of heroic fighting available within each group. Consistent with the "imbalance of power" hypothesis developed by biologists and primatologists (Alexander, 1979; Wrangham, 1999a)—as well as with Napoleon's comment that "God is on the side of large armies"—the larger group will win when the mean propensity to altruism is equal across two contending groups. However, a smaller population *can* defeat a larger one if its members are substantially more altruistic (hence more heroic).

Death. Some proportion of the defeated group is killed, and we will report our findings initially from the strong assumption that *all* are killed, thus that defeated populations are eliminated from the evolving population. We should remember that, while this extreme case is certainly reflected in the historical record (Potidaea, Mytilene, and Melos in the Peloponnesian war, for example), victorious groups, when considering how to treat those they have defeated, are also capable of keeping a strategic eye on the resource gains (females as well as land) that are more or less available to them as a result of their efforts. As Betzig (2005, p. 335) sets out the Biblical case from Deuteronomy 20:13-17:

> God handed Moses two different laws about spoils. One was for wars with close neighbors; the other was for more remote wars. When their enemies lived far away, he said, 'you shall put all the males to the sword, but the women and the little ones, the cattle, and everything else in the city, all its spoil, you shall take as booty for yourselves.' But when their enemies lived nearby, 'you shall save alive nothing that breathes, but you shall utterly destroy them.' Land was the limiting factor.

We explore the importance of this "genocide" parameter analytically in a later section.

In the simulation, members of the victorious group migrate to the newly captured territory such that per-capita resources in the two areas are equalized. Once migration is complete, no "memory" of prior ties persists, so the two "daughter" groups created by the schism are just as likely to attack one another in subsequent rounds as they are to attack a different group.

Variation. Selection on altruism—as on any other attribute—can, of course, only happen in the context of variation in that attribute. As noted, members of each group vary in altruism at the start of the simulation. During reproduction, there are two mechanisms by which variation is maintained. One models random mutation (defined as M_1 in the appendix). By default, mutation occurs in less than one percent of offspring, and can result in the offspring having an altruism level quite different from the parent. The other (defined as M_2) simulates (without directly modeling) sexual reproduction, such that offspring resemble their parent within a range of variability.

Model 2: Domain specific with both "communitarianism" and "heroism"

The second simulation has the same structure as the domain general one, except that each individual is characterized by two domain specific altruistic propensities, heroism and communitarianism, each similarly modeled as varying between 0 and 1. Starting mean heroism and communitarianism for each group are separate parameters of the model. Member levels for the two attributes are independently drawn from a uniform distribution centered at the specified mean. Reproductive costs from communitarianism are paid every generation; those from heroism are paid per war.

Method

We ran 10,000 simulations of each of the two models. To ensure that the data we report reflect a wide variety of possible evolutionary environments, the following parameters were drawn randomly[5] for each run:

1. Each group's resource endowment (R_g)—specified separately for each group;
2. Baseline fitness—the probability of reproductive success for all agents before the consequences of altruism, communitarianism, heroism or warfare are incorporated (P_b);
3. The fitness advantage to group members from an individual's communitarianism (P_c);
4. The cost to the individual agent of its communitarianism (C_C);

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[5] From a multivariate uniform distribution with an identity correlation matrix with $R_g \sim \mathrm{U}[50,100]$, $P_b \sim \mathrm{U}[0,0.5]$, $P_C \sim \mathrm{U}[0,0.5]$, $c_C \sim \mathrm{U}[0,0.1]$, $c_H \sim \mathrm{U}[0,0.1]$, $S_A \sim \mathrm{U}[0,1]$ (S_C, S_H for the two attribute model), $M_1 \sim U[0,0.005]$, $M_2 \sim U[0,0.05]$.

5. The cost to the individual agent of its heroism (C_H);
6. (In Model 1) Mean starting altruism (S_A);
7. (In Model 2) Mean starting communitarianism and heroism (S_C, S_H);
8. The two sources of variation (two types of mutation) in the attributes of offspring as specified in the appendix (M_1, M_2).

Two parameters were fixed across all the simulations: the survival threshold, $T = 1$ (one unit of resource per capita), and the number of groups, which was always four.[6]

Each simulation was run for 1100 generations, with the first thousand generations in each case discarded to ensure that the system had evolved away from the diverse starting values. For the last 100 generations we recorded simulation parameters and a *moving average* of the dependent variables—altruism in the domain general model, and communitarianism and heroism in the domain specific model. We also recorded the frequency of wars across all generations for each run. We ran 10,000 simulations for each model recording in each case the simulation run parameters (sampled as described above) and the moving average for the relevant dependent variables.

In smaller sample of runs to check for the system's sensitivity to some of our choices, we increased the number of generations and varied both the number of groups and the length of the moving average across which we recorded data. None of these modifications affected our substantive results.

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[6] Four is an arbitrary number; running the simulation with two, three and more than four groups made no fundamental difference to our findings.

Findings

With the domain general model we observed a modest but significant selection on altruism. This is shown in Figure 1, which is a frequency distribution for evolved altruism. The horizontal axis specifies the altruism level averaged across the last 100 generations and the vertical axis records the density of cases across the randomized parameter space. The mean altruism value in this positively skewed distribution is 0.25 (the median is 0.17), interpretable as the mean individual being 25% altruistic—or, alternatively, that the mean individual would have a .25 probability of contributing to group members' fitness, thus to the group's population growth, via its communitarian activities *and* a .25 probability of fighting heroically in any war that its group had to fight.

Despite the fact that both behavioral components of the general purpose attribute altruism are reproductively costly to individuals, therefore, we do observe some selection on that attribute. Agents pay a reproductive cost proportional to the strength of their generalized disposition to altruism, but this cost is outweighed by the benefits the individual reaps from the group's success in warfare. Multiple regression of ending altruism values on parameters in the model shows a negative association between evolved altruism and (1) the cost of altruism, (2) the average size of group resource bases (hence, the average size of groups), and (3) variation in resource base size (hence, variation in size among the groups); it also shows a positive association between altruism and the frequency of war (see Appendix II). This suggests that higher (and less typical) evolved values of altruism occurred in runs in which the cost of altruism was low, groups were smaller and more equal in size, and wars were frequent.

With the domain specific model, in which communitarianism and heroism were free to evolve as separate attributes, Figures 2a and 2b show that: (1) heroism evolved to substantially higher levels than communitarianism with means of 66.9% and 30.5% and medians of 70.3 and 22.6 respectively, and (2) *both* attributes evolved to significantly higher levels than did altruism in the domain general model. There are, therefore, three findings to be explained—first, the fact that there was *some* positive selection on general purpose altruism, despite its costs to the individual; second, the stronger selection on heroism than on communitarianism; and third, that when communitarianism and heroism are free to evolve separately, both evolve to higher levels than when they are combined as expressions of a single, general purpose altruism attribute. We will address the evolution of general purpose altruism (the first finding) shortly; first we discuss the relative evolution of the two domain specific forms (findings two and three).

***Why does heroism evolve to higher levels than communitarianism*?**

To this point in the analysis, heroism has only entailed a cost in the event of war. Given that war is only a sometime thing[7] while communitarianism occurs in every generation, perhaps heroism evolves to a higher level simply because the cost of heroism is paid less frequently than the cost of communitarianism.

This does appear to be part of the story. Figure 3 reports the distribution of heroism when the cost of heroism is paid every generation rather than only in the event of war. With the mean of this distribution now at .475 (as opposed to .669 in the original model), clearly this cost difference accounts for some of the relatively greater selection on heroism—but it is *only* part of the story, since the mean of heroism is still substantially higher than the .305 mean of communitarianism in the original model.

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[7] In fact, averaged across all runs, it happens to any given group with a probability very close to .5 in every generation.

Another part concerns the immediacy of the benefits to fighting capacity that a group reaps from communitarianism and heroism. Since reproduction happens at the end of each generation, communitarianism increases the number of fighters a group will be able to field in the *next* generation while heroism increases a group's fighting capacity in the *present* one. Thus communitarianism can only increase a group's *future* fighting ability—assuming the group survives any wars in the current generation, which will depend on group size and heroism *now*. Notice that the delayed effect of communitarianism is consistent with real-life population dynamics; since infants and young children confer no advantage in war, the war-fighting benefits of increased fertility cannot be realized immediately.

Communitarianism is also a "two-edged sword" for a group's fighting ability. While it does contribute to a group's (future) fighting ability, its effect on population growth can also be responsible for getting that group *into* war in the first place—in which case there is some chance of its losing, thus of consequent selection *against* communitarianism. Heroism, on the other hand, is an unambiguous good for a group: In the absence of war—and assuming its cost is only paid in the event of war—it does no harm to the individual or the group, but in the event of war it *can* be decisive in allowing the group to win.

Ultimately, selection on communitarianism and on heroism must be a function of whether the behavior produced by those dispositions is "critical" to the group's success in warfare, and while both contributions *might* be critical for the outcome of a given war, it appears that heroism is more likely to be critical than communitarianism.

Why, then, does altruism evolve?

The positive selection on general purpose altruism in the single attribute model, modest as it is, can now be explained in the same way as selection on heroism and communitarianism in the two attribute model. Altruists fight for their groups, and a given altruist's fighting *can* be critical for the group's survival, thus for the altruist's own survival. Similarly—although with a lower probability—an altruist's communitarian behaviors might also be critical for such survival via the role that numbers *as such* can play in outcome of wars.

Why do communitarianism and heroism evolve to higher levels than general-purpose altruism?

An unexpected finding was that when they are allowed to evolve independently, *both* communitarianism and heroism evolve to higher levels than does the single, general purpose attribute altruism.[8] Why do both functions evolve more rapidly when they are performed by two independent mechanisms than when they are performed by a single, general purpose mechanism?

In retrospect, at least, the explanation is clear. When a single, general purpose mechanism performs two distinct functions (A and B), both of which decrease individual fitness, selection against that mechanism based on the costs of A will also select against performance of B, and vice versa. Conversely, when there are two special purpose mechanisms performing A and B, selection based on the individual costs of B has no implications for selection based on the costs of A, and vice versa. Thus, breaking the general purpose mechanism down into two special purpose mechanisms means the evolution of one attribute is not handicapped by the cost of the

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[8] Outcomes of the multiple regression analysis (see Appendix II) indicate a zero correlation between mean evolved communitarianism and heroism values. Hence a more general tendency toward altruism did not evolve; nor was there any evidence of an evolved tendency of agents to "specialize" in one or the other form of domain-specific altruism.

other, improving the strength of group versus individual selection in the accounting of multi-level selection. Heroism, which is invoked only every second generation or so, benefits much more from such “de-linking of costs” than does communitarianism, which is invoked—and thus, if linked, extracts a cost on heroism—in every generation.

This finding with respect to the probable “cognitive architecture of altruism” is not, in itself, an answer to the classic problem of how privately costly altruistic dispositions might evolve; each disposition must be positively selected despite the costs that it generates for the acting individual. But the finding does raise the possibility that thinking about altruism as a bundle of special purpose forms of *altruist behaviors*—each evoked in some circumstances but not in others—and not as a single general purpose disposition evoked regardless of the contextual specifics, will prove a fruitful path to follow.

Does heroism depend on “constant” battles?

The case for humans’ past being one of “constant battles” becomes increasingly difficult to make the further back in time one looks and, as discussed above, this has fueled arguments about just how “constant” warfare—however that might be defined—actually was in our ancestral past. Whatever the facts of the matter, our findings about the evolution of heroism turn out not to be critically dependent on the frequency of warfare. For the simulation data, we regressed mean heroism for the last 100 generations on the overall frequency of war.[9] Even with the power afforded by an *n* of 10,000, the coefficient for number of wars was not significant (see

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[9] Along with other key input parameters that varied across the runs such as cost of heroism, the size of the resource base and variation in resource base size between groups. These were all significant *negative* predictors of heroism.

Appendix II). As long as war does occur at least every *few* generations, it appears that heroism will evolve in response, and that such evolution is not affected by any greater frequency of wars—even should there be as many as several per generation.

One strong assumption of both simulations, which allowed us to model a period in human history in which groups remained relatively modest in size, was the assumption that all members of defeated groups were killed (or otherwise removed from the population—for example, by fleeing the territories occupied by our simulated groups). To examine the impact of this "casualty" rate in defeated groups, we turned to an analytic model.

An Analytic Model of Heroism

Although our simulations make a range of simplifying assumptions, they are still more complex than what can be readily modeled analytically. Accordingly, we have used a simplified analytic model to explore in a more rigorous fashion the impact of a few key parameters on the evolution of a propensity for heroism. The cost of this precision was to reduce the number of groups from four to two equally sized groups and to model heroism as a dichotomous variable with each agent being either fully heroic or a complete coward. (See Appendix III for a formal description of the model.)

As noted above, the simulation results are based on the strong assumption that a defeated group is entirely wiped out—that victors practice *genocide* on losers or, functionally the same from an evolutionary point of view, that the victors prevent the losers from reproducing (as, potentially, in slavery, for example)[10] or that the losers otherwise vanish from the population of

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[10] In our simulation, genocide in the event of defeat is the only way that agents die. When we tried reducing the level of genocide, exponential population growth and constant war was the

interest, perhaps by migrating to a distant territory. Although the archeological record does suggest that genocide was at least *sometimes* practiced (Keeley, 1997; LeBlanc & Register, 2003) and the elimination of a competing group has been documented in a chimpanzee population (Wilson & Wrangham, 2003), we simply do not know just *how* pervasive this outcome was. Nevertheless, one potentially problematic consequence of the strong genocide assumption in our simulations is that a hero whose efforts are critical for his own side's victory is also averting, with certainty, his own death in defeat. What happens to selection on heroism when that assumption is relaxed?

In the analytic model, any individual's probability of surviving a war is defined by $1 - dG$, when d is the probability of the group's being defeated (a function of the relative summed heroism scores in the contending groups) and G is the proportion of the defeated group that is killed (the genocide parameter). At one extreme, therefore, if the genocide parameter is 1.0 (the entire defeated group will be killed), then an individual hero's actions *can* be critical not only for the group's survival, but also for his own—as in the simulation. At the other extreme, if the genocide parameter is zero then all individuals survive the war despite their defeat,[11] and a hero's actions, while costing him personally in reproductive terms, do not promote his own

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result, along with a vastly increased demand on computational resources that made large numbers of runs of 1000 generations impractical. With $G = 1$, however, population size remains more or less constant, cycling around the same mean. Accordingly, for this analysis of genocide, we have relied exclusively on the analytic results.

[11] Note that we are equating "surviving the war" with retaining the potential for reproduction—not inevitable, of course, in the event a defeated population is enslaved. In our evolutionary model retaining the potential for reproduction is the critical issue.

survival. In short, heroism is more likely to evolve when genocide (or at least, a very high casualty rate) is the outcome for defeated groups, *ceteris paribus*.

The analytic model demonstrates that the equilibrium proportion of heroes, $q*$, at which it is equally beneficial to be a hero or a coward, depends not only on genocide rates, but also on the overall population size, n (Figure 4, see also Proposition 3 and related proof in Appendix III). As the population size increases, the slope of the curve flattens and the equilibrium proportion of heroes for a given level of genocide declines. Intuitively, the larger the population, the less likely it will be that any given heroic contribution will be critical to the group's survival—thus also to the survival of the hero himself. The result is, of course, compatible with the well-recognized relationship between group size and the rationality of contributing to public goods in general (Buchanan, 1968; Olson, 1965).[12] It also matches the finding from the simulation results that heroism evolves to higher levels when groups are smaller.

The analytic results indicate (and Figure 4 illustrates) that the equilibrium proportion of heroes falls off steeply as the casualty rate for the losing side declines from complete genocide to most group members surviving (toward the left of the graphic). If we assumed that casualty rates were unbiased across that distribution—and, as we have argued, we simply don't know the facts of the matter—it would follow that the selective pressures of war favored the evolution of

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[12] In the analytical model, the total population consists of two groups, so the curves in Figure 4 correspond to group sizes of 25, 50, and 100. In the simulation runs reported above (in which G =1), the average resource base size (which constrains group size) was 75 (and ranged from 50 to 100), with mean evolved values of heroism of .475 and .669, depending, respectively, on whether the cost of heroism was paid per generation or per war.

heroism as a relatively rare phenomenon among humans (or, at least, as a low probability behavior among all individuals).

Summary and Conclusions

Using simulation, we have shown that heroism—a willingness to fight for one's group even when it places oneself at a reproductive disadvantage relative to other group members—can evolve within a population of groups that, at least sometimes, go to war with each other over scarce resources needed for individual and group survival. The simulation in which agents are characterized by a general purpose altruism supporting both "communitarianism" and "heroism" produces modest positive selection on that attribute. When agents are characterized by two independent, special purpose attributes heroism and communitarian, however, *both* of those attributes evolve to higher levels than does general purpose altruism, with heroism evolving to substantially higher levels than communitarianism.

An altruistic attribute can only evolve when the individual's action returns greater *private* reproductive benefits than reproductive costs, and in the case of heroism, that is more likely (1) in relatively small groups when one individual's heroism is more likely to make the difference between victory and defeat for the group; and (2) when defeat means a high probability that everyone, the hero included, will be killed by the victorious group. Communitarianism *can* contribute to a group's victory, thus to positive selection on communitarianism itself, since with heroism constant, larger groups will be more likely to win a war than smaller ones. But heroism is more strongly selected in part because of the immediacy of its impact on a group's success in war and in part because communitarianism is a "two edged sword" that *can* contribute to victory, but can also be responsible for triggering a war that the communitarian's group could quite possibly lose.

Our unexpected finding that communitarian and heroic dispositions, when modeled as separate, domain specific attributes, both evolve to higher levels than the domain general disposition altruism suggests a more general cost-benefit argument for the efficiency of modular design beyond the standard argument that a design that is optimal for solving one processing problem will seldom be optimal for solving another. Given that all adaptations involve costs (energy resources that could be used otherwise), modularity allows costs associated with solving one problem to be paid without qualifying the organism's success in solving a second problem, which is what happens with general purpose designs.

There are, of course, other adaptive rewards to heroism beyond the possibility of one's action being critical for one's own survival. Most obviously, as mentioned above, the group's success can mean male members' access to the inherently scarce reproductive capacities of defeated females via rape and capture. Also, to the extent ancestral groups consisted substantially of relatively close kin, the theory of inclusive fitness (Hamilton, 1964) suggests how "genes for heroism" could be passed on through the survival of the hero's relatives, even should the hero himself *not* survive; supporting this, it is certainly true that *political rhetoric* seeking to mobilize heroism in large, complex modern societies often invokes kinship (G. Johnson, 1987). And cultural evolution can provide a wide range of rewards for heroic behavior including fame, honor, and money, all of which can translate readily into reproductive success. Our analysis certainly does not discount the evolutionary importance of any such processes in explaining human males' willingness, even eagerness, to go to war—and their willingness, even eagerness, to engage in highly risky behavior while doing so.

The model's conclusion that heroism should evolve to higher levels in a population of smaller groups is, however, nicely consistent with estimates that social life in our remote past was organized in groups whose size varied between only a handful to, perhaps 250 individuals at the outer limit (Dunbar, 1993, 1996). In such an environment, one individual's heroism *could* be the salvation of his group—at least sufficient to tip the balance given the relative incidence of heroism in two battling groups. And although we cannot know with certainty about the incidence of genocide in that past, it is surely more likely that all members of a small group would be wiped out in the course of a war (or die off later as a consequence of defeat and the loss of resources and reduced group size) than those of a big one—making two of the conditions that we have identified as critical to the evolution of heroism during humans' remote past almost certain to have been in place.

That frequent warfare was also in place is, as we have indicated, the subject of some dispute among anthropologists, and there must certainly have been extensive periods when resource competition was substantially absent as a cause of warfare—or, at least, when migration was a relatively costless alternative to fighting over existing resources. But the absence of a correlation between heroism and the frequency of warfare makes that argument irrelevant to the case presented here. Even a little warfare, so our simulations suggest, would have gone a long way toward selection on heroism as an attribute of our ancient ancestors.

Appendix I. The Formal Structure of the Simulation.

A territory $g = 1, 2, ...$ is endowed with R_g natural resources and is populated by a number of individuals, n_g, who form a group that consumes the territory's finite resources. Each territory's resources define the limit of how many people it can support, the exogenous survival threshold, $T : R_g / n_g > T$. Should population growth cause a group's resources per capita to fall below that threshold, it declares war on another group, randomly chosen.

Groups must fight if attacked. Each member of a group can increase that group's fighting strength by active fighting in a war, the behavior we term "heroism." As with communitarianism, we assume that heroism decreases the probability of an individual's having offspring by $y > 0$, with cost proportional to the level of heroism. Heroism is also a continuous variable, $h_i \in [0,1]$. The group with the greater fighting strength, $\sum_{i=1}^{n_g} h_i$, wins a war. Members of the losing group die or—functionally the same—vacate the broader ecology. 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.

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 fertility for the group g becomes $P_b + P_c A_g$, where $P_c > 0$ is the difference between purely communitarian and non-communitarian groups, and $A_g = \frac{1}{n} \sum_{i=1}^{n_g} c_i$ is the group's average communitarianism, with $c_i \in [0,1]$ being the propensity to communitarian behavior of a given member i. Communitarianism is costly to fertility, decreasing the probability of an individual's having an offspring by $x > 0$; the cost is assessed proportional to c_i. In each generation an individual i reproduces depending on its probability of having an offspring. Reproduction is asexual and stochastic. It is also subject to mutation: Offspring' attributes are copied from the parent subject to a uniform shock with zero mean and an exogenous variance. In addition, with a very small exogenous probability, offspring attributes can be drawn from a uniform distribution $\mathrm{U}[0,1]$.

Combining the factors above, the probability of member *i* of a *surviving* group having an offspring is $P_b + P_c A_g - c_i x - h_i y w$, where $w = 0,1,...$ 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 relatively more communitarianism and heroic grow faster. Faster growth means the group will reach the limits of its resource base more rapidly, but larger groups are also more likely to win wars. The domain general model is identical except that $c_i \in [0,1]$ is *both* a propensity to communitarian behavior *and* to heroic participation in wars.

Appendix II. Multiple Regression.

Statistical analysis of the multiple simulation runs provides further evidence that cooperation and heroism are two distinct forms of altruism, subject to distinct adaptive pressures (Table AII.) Growth difference describes the growth advantage that more cooperative groups have over less cooperative groups. In general, the larger the growth difference, the sooner more cooperative groups will become overpopulated, experience resource stress, and attack other, possibly less populated, groups. In the two attribute model this variable has a significant positive effect on the evolution of cooperation, but a significant negative effect on the evolution of

Table A.II. Effect of parameters of environment on altruism, cooperation, and heroism

Dependent Variable	Altruism	Cooperation	Heroism
Growth Difference	0.003	0.061**	-0.008*
Wars	0.497**	0.404**	-0.001
Cost (Altruism)	-0.373**		
Cost (Cooperation)		-0.572**	-0.001
Cost (Heroism)		-0.003	-0.183**
Resources Mean	-0.322**	-0.513**	-0.115**
Resources Std. Dev.	-0.170**	-0.049**	-0.144**
Constant	-0.381	-1.135**	-0.265
Observations	9950	9919	9919
R-squared	0.63	0.55	0.19

heroism. In the one attribute model, however, growth difference appears to have no effect on the evolution of altruism. The reason for this difference is that, in the two-attribute case, wars can be decided by a difference in group size that swamps the impact of heroism—viz., a large group of not-so-heroic fighters can defeat a small band of more heroic ones. In the one attribute case, however, generalized altruism captures both (opposing) effects, making the growth difference falsely appear insignificant.

Dependent and independent variables are analyzed in the form of natural logarithms. In double log form, regression coefficients can be interpreted as elasticities measuring the percentage change in the dependent variable for a one percent change in an independent variable with other variables constant. Other statistical specifications lead to substantively similar results. One star indicates significance at 5%; two stars indicate significance at 1%. Cases when the dependent variable was zero were dropped from the double log specification.

Appendix III. An Analytic Model of Heroism.

The following simple analytic model specifies the logic by which multi-level selection via warfare can select for the individual attribute heroism.

Imagine a world with two equally-sized groups. In this simple world, heroism is a binary variable—there are only heroes and non-heroes. All individuals, regardless of their type, have a baseline fitness $P_b \in [0,1]$. Heroism, however, is costly whenever invoked, and thus decreases a hero's baseline fitness by $c > 0$. Therefore, the fitness of a hero is $P_H = P_b - c$; conversely, the fitness of a non-hero is $P_{\sim H} = P_b$. Clearly, *within a group* the fitness of non-heroes is always greater than the fitness of heroes, $P_{\sim H} > P_H$, as long as $c > 0$.

Can heroism evolve? To answer this question we introduce *between-group* competition. Assume that the two groups in the model periodically fight with each other and the group with more heroes wins the conflict. Members of the winning group survive while losers die out completely; they are the victims of genocide. Thus, although at the individual level we have a clear selection on non-heroism, at the group level we have a clear selection on heroism.

Define d as an exogenous probability that a group to which an individual belongs will be defeated in a war if this individual does not fight, i.e., *not* a hero. The probability d is a function of the distribution of heroes across the whole world. Being a member of the defeated group, however, does not guarantee death. If genocide is not total, some members of the losing group will survive the war. Let $G \in [0,1]$ describe the proportion of those in the defeated group who are killed. When G = 0, everyone in the losing group survives; when G = 1, everyone in the losing group dies. As a result, a non-hero's baseline fitness, P_b, is contingent upon the likelihood of surviving a war, $(1 - dG)$:

(1) $$P_{\sim H} = P_b\left(1 - dG\right).$$

By being a hero, an individual may affect the likelihood that his group wins a war, thus allowing all members—himself included—to survive, but such heroic behavior comes at a personal reproductive cost. The particular impact that an individual's heroism has on his group's likelihood of winning a war depends on the number of people fighting heroically. For example, if there are no other heroes at all, an individual will decide the outcome of war by himself—with certainty. On the other hand, if heroes are common, an individual's impact may be trivial. Define q as a proportion of heroes in the world (across the two groups)

(2) $$q = \frac{1}{n}\sum_{i=1}^{n} h_i ,$$

where n is the total world population, and $h_i = [0,1]$ is the type of individual i, 1 if a hero, 0 if a non-hero. Using combinatorics we can establish that the probability that an individual hero will make a difference to the outcome of a war is

(3) $$v = \binom{qn-1}{\left(qn-1\right)/2} 2^{-\left(qn-1\right)},$$

which can be approximated by $v = \frac{1}{\sqrt{qn}}$.

If an individual is not decisive, then his fitness is weighted by the exogenous probability of survival $\left(1 - dG\right)$. However, when an individual is critical, his group wins and the probability of survival is 1. Thus, the expected fitness of a hero is equal to:

(4) $$P_H = \left(\left(P_b - c\right)\left(1 - dG\right)\right)\left(1 - v\right) + \left(P_b - c\right)v .$$

The first term in the formula describes a case when the hero is not decisive and the second term describes a case when he is.

When $v \to 0$, i.e., a hero is extremely unlikely to be decisive, the fertility of cowards, $P_{\sim H} = P_b\left(1-dG\right)$, is dominating the fertility of heroes, $P_H = \left(P_b - c\right)\left(1-dG\right)$.

When $v \to 1$, i.e., a hero is decisive, the fertility of heroes, $P_H = P_b - c$, is greater than fertility of cowards, $P_{\sim H} = P_b\left(1-dG\right)$, if $c < P_b dG$.

For all other cases, evolutionary success of a type depends on the criticalness of heroism $v = \frac{1}{\sqrt{qn}}$. Using expressions (1) and (2), we can establish when the population becomes homogeneously non-heroic, $P_{\sim H} > P_H$, homogeneously heroic, $P_H > P_{\sim H}$, or heterogeneous $P_H = P_{\sim H}$. The fitness formulas (1) and (2) were derived without taking into account group membership. However, since an individual is equally likely to belong to either of the groups, the fitness formulas for heroes and non-heroes across the two groups become:

(5.1) $P_H = \left(P_{H,1} + P_{H.2}\right)/2$,

(5.2) $P_{\sim H} = \left(P_{\sim H,1} + P_{\sim H.2}\right)/2$,

where

(6.1) $P_{H,1} = \left(\left(P_b - c\right)\left(1-dG\right)\right)\left(1-v\right) + \left(P_b - c\right)v$,

(6.2) $P_{H,2} = \left(\left(P_b - c\right)\left(1-\left(1-d\right)G\right)\right)\left(1-v\right) + \left(P_b - c\right)v$,

(6.3) $P_{\sim H,1} = P_b(1-dG)$,

(6.4) $P_{\sim H,2} = P_b(1-\left(1-d\right)G)$.

The expressions 6.1 – 6.4 describe the fitness of heroes and non-heroes belonging to groups 1 and 2. For example, $P_{H,1}$ is a fitness of a hero from group 1.

Using (5.1) and (5.2) we can solve for an equilibrium proportion of heroes in the whole population, q^*. Since an individual is equally likely to belong to either group, assume that $m = 0.5$. Then there is a unique equilibrium:

(7) $$q^* = \left(\frac{G(P_b - c)}{(2-G)c\sqrt{n}} \right)^2.$$

Figure 4 in the main text represents the equilibrium proportion of heroes q^* as a function of genocide G at different population sizes.

Having found the equilibrium proportion of heroes in the population, we can characterize the equilibrium in greater detail making several propositions.

Proposition 1: The equilibrium proportion of heroes q^* is evolutionary stable.

Proof. The equilibrium proportion of heroes in the world, expression (7), solves $P_H = P_{\sim H}$, where P_H and $P_{\sim H}$ are defined as in (5.1) and (5.2) respectively. The solution is unique. $q^* < 0$ implies that the equilibrium proportion of heroes in the world is strictly zero. $q^* > 1$ implies that the proportion is exactly one.

The unique equilibrium is evolutionary stable. Any minor deviations from the equilibrium proportion result in return to the equilibrium. Since $P_H > P_{\sim H}$ for all $q < q^*$, and $P_{\sim H} > P_H$ for all $q > q^*$, we have an evolutionary stable equilibrium q^*. Graphically, the evolutionary stability of the equilibrium is shown in Figure A.III.

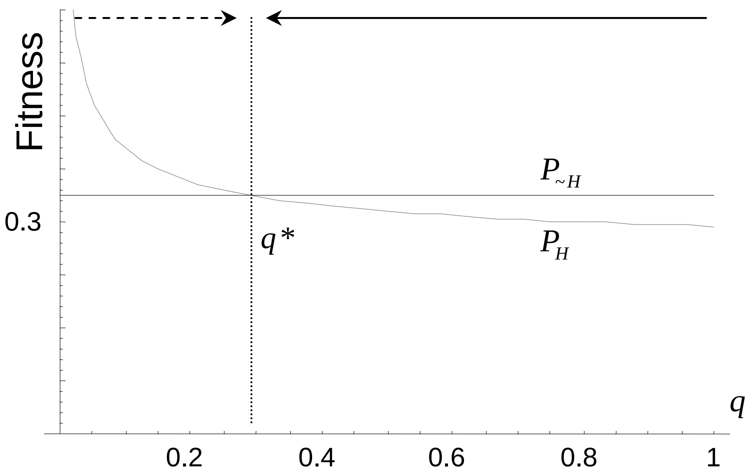

Figure A.III. Illustration of the equilibrium proportion of heroes q^*. Fitness of heroes, P_H, and non-heroes, $P_{\sim H}$, as a function of q, the proportion of heroes across both groups. The equilibrium is evolutionary stable because of the converging dynamics.

Proposition 2: There is a homogeneously non-heroic population only when either

(1) There is no killing in wars.

(2) The cost of heroism is equal or greater than the baseline probability of having an offspring.

Proof. Evident from (7): $q^* = 0$ when $G = 0$ or $P_b = c$.

Proposition 3: The equilibrium proportion of heroes is increasing in genocide and baseline fitness, and decreasing in the population size and the cost of heroism.

Proof. Using the equilibrium formula (7) we can derive the following comparative statics:

$$\frac{\partial q^*}{\partial G} = \frac{G\left(2P_b - 2c\right)^2}{\left(2-G\right)^3 nc^2} > 0, \quad \frac{\partial q^*}{\partial P_b} = \frac{G^2\left(2P_b - 2c\right)}{\left(G-2\right)^2 nc^2} > 0,$$

$$\frac{\partial q^*}{\partial n} = -\frac{G^2 \left(P_b - c\right)^2}{\left(G-2\right)^2 n^2 c^2} < 0\,,\ \frac{\partial q^*}{\partial c} = \frac{2P_b G^2 \left(c - P_b\right)}{\left(G-2\right)^2 nc^3} < 0\,.$$

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Figure 1.

Density distribution of evolved altruism in the one-attribute model. Mean altruism = 0.250.

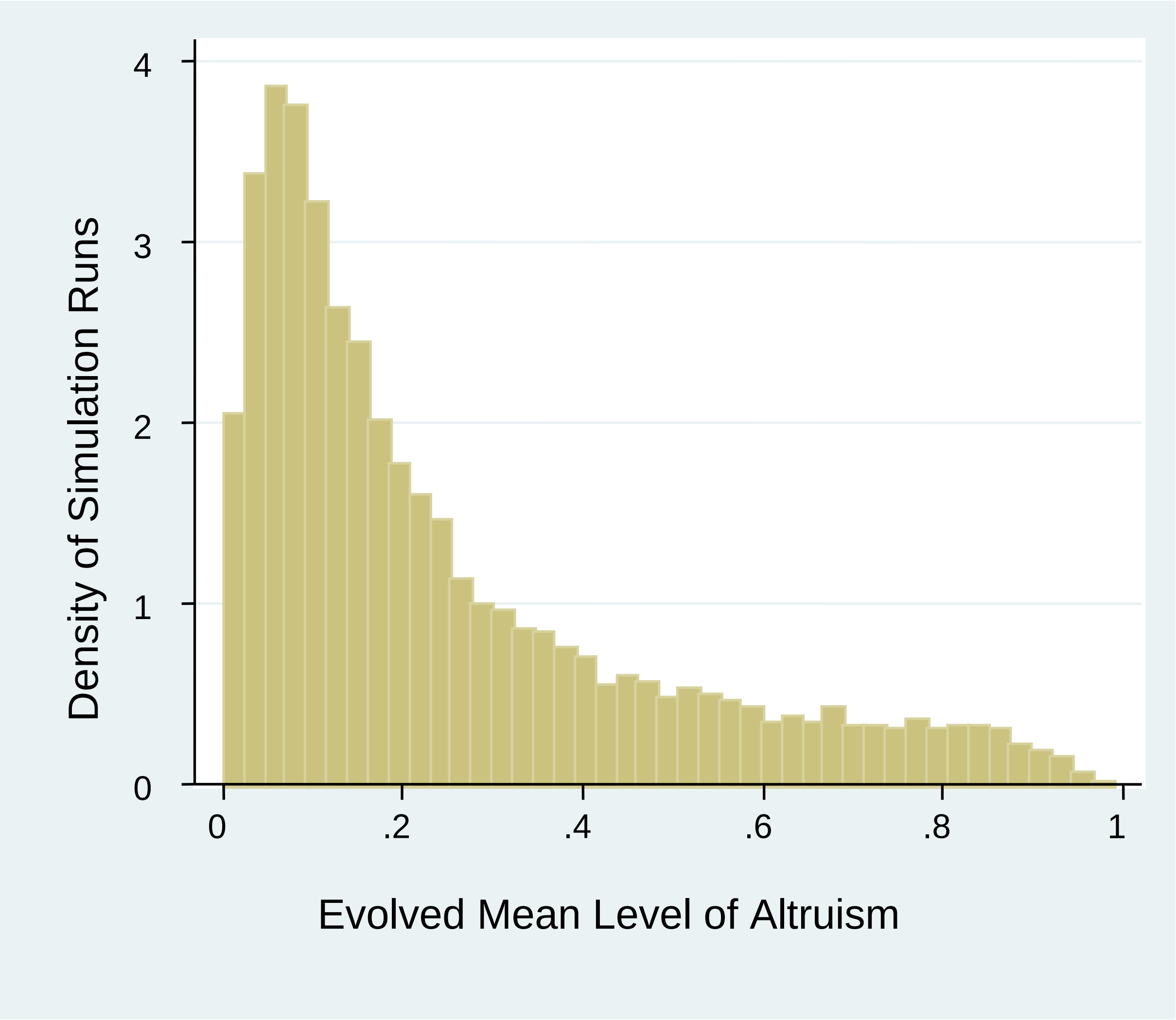

Figure 2a.

Density distribution of evolved heroism in the two-attribute model. Mean heroism = 0.669.

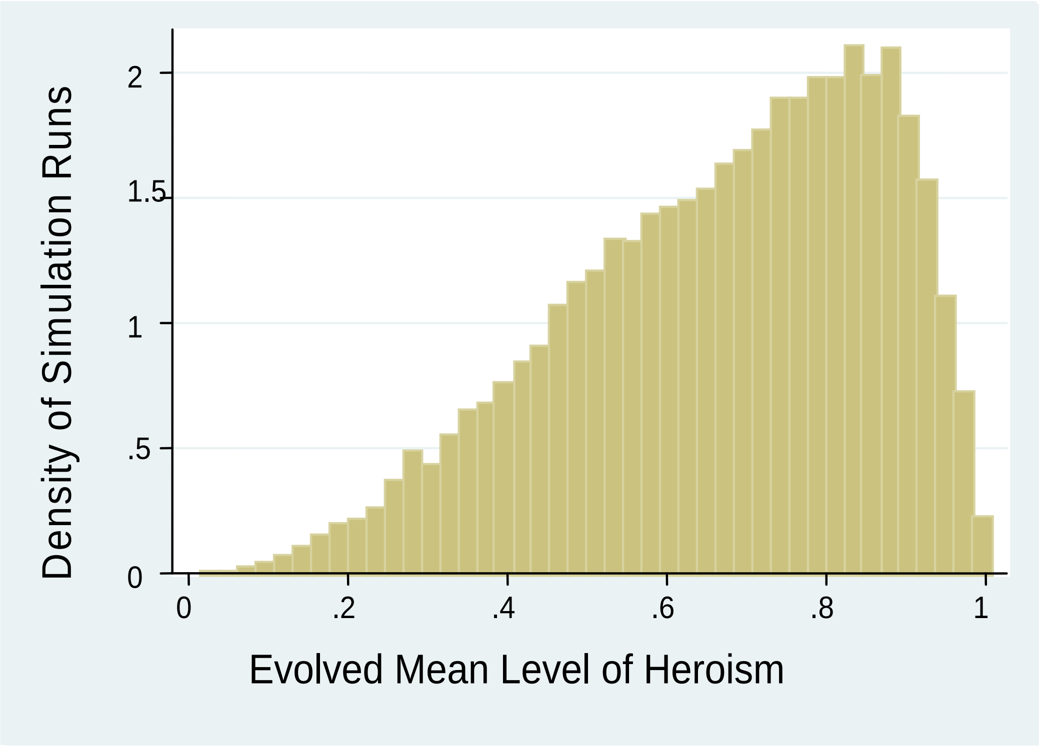

Figure 2b.

Density distribution of evolved communitarianism in the two-attribute model. Mean communitarianism = 0.305.

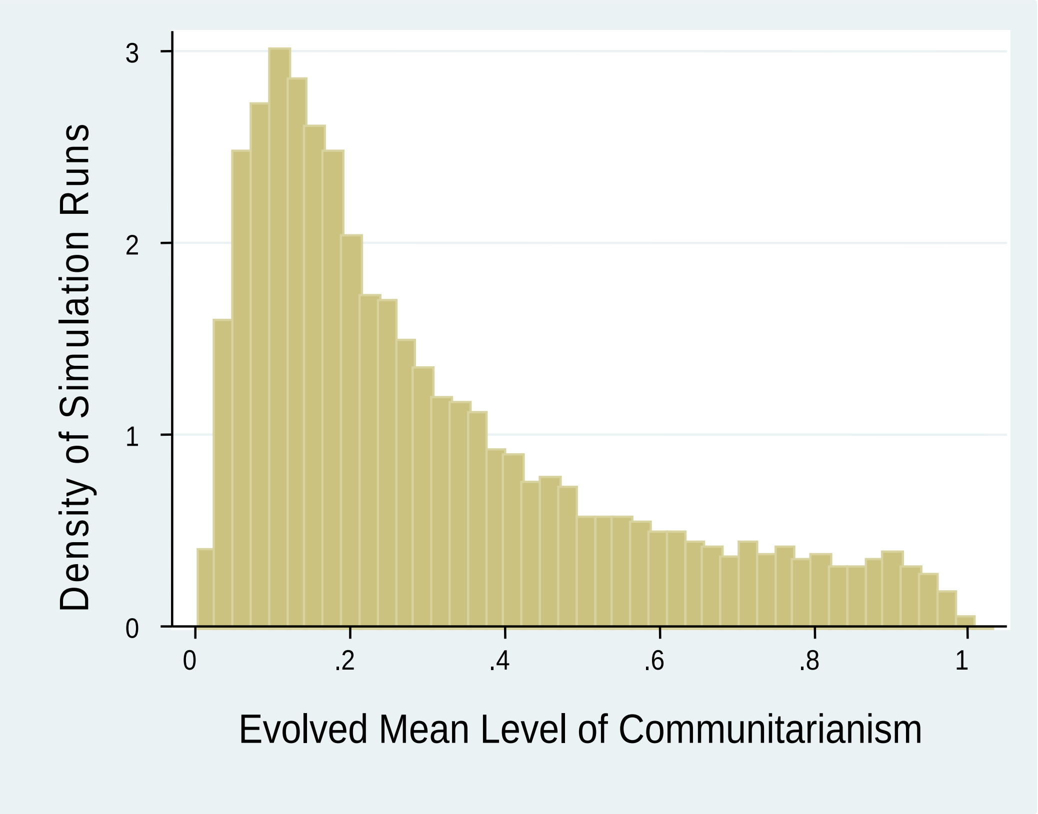

Figure 3.

Density distribution of evolved heroism in when the cost of heroism is paid every generation. Mean heroism = 0.475.

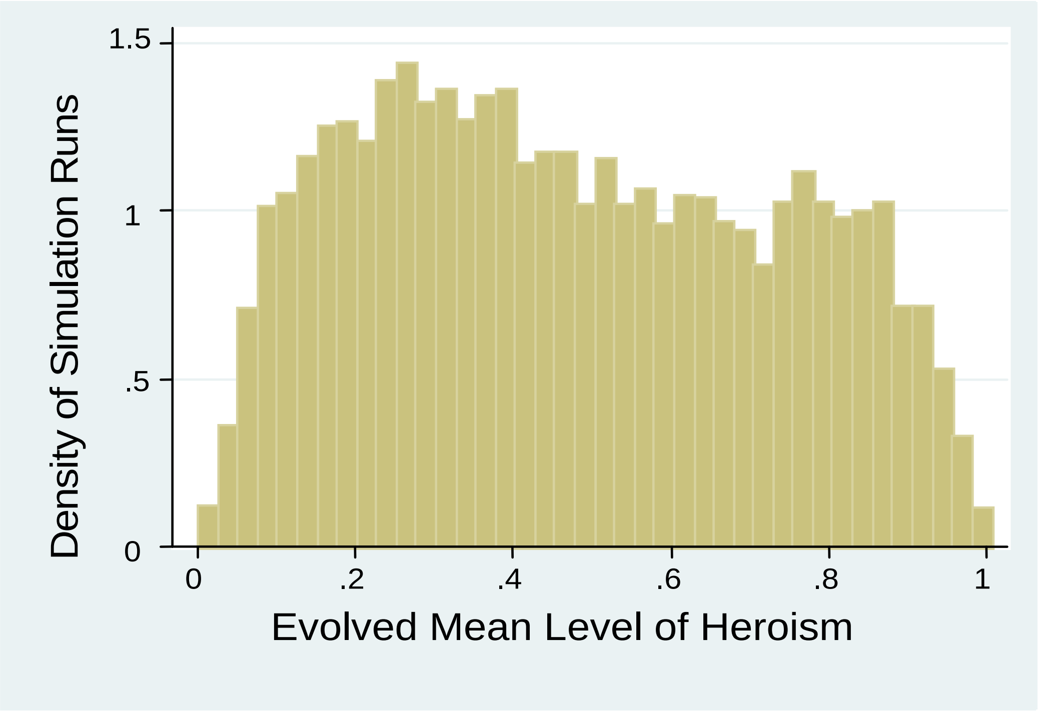

Figure 4.

Equilibrium proportion of heroes q^* across two groups as a function of genocide G for three different population sizes *n*, $P_b = 0.5$, $c = 0.05$.