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Ancestral War
And the Evolutionary Origins of 'Heroism'

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Ancestral War

And the Evolutionary Origins of 'Heroism'

“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

Primatological and archeological evidence along with anthropological accounts of hunter-gatherer societies indicate that lethal between-group violence may have been sufficiently frequent during our ancestral past to have shaped our evolved behavioral repertoire. Two simulations explore the possibility that *heroism* (risking one's life fighting for the group) evolved as a specialized form of altruism in response to war. We show that war selects strongly for heroism but only weakly for a domain-general altruistic propensity that promotes both heroism and other privately costly, group-benefiting behaviors. A complementary analytical model shows that domain-specific heroism should evolve more readily when groups are small and mortality in defeated groups is high, features that are plausibly characteristic of our collective ancestral past.

When Homer asks at the outset of 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; 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, polis, 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 heroic actions in warfare have focused on “proximate” answers—emotional, cognitive or other mechanisms that prompt such behavior in the here and now. Thus, for example, loyalty to small groups of fighting comrades (Gat 1999; Shills and 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 (Johnson 2004; Johnson et al. 2006; Wrangham 1999b) have all been argued to support such behavior. By the same token, social psychologists have identified many mechanisms likely to be implicated in humans’ frequent xenophobic willingness to engage in hostile action against other groups—most famously, the ease with which we categorize others into “in-group” and “out-group,” favoring the former and, often, demonizing the latter (Ackerman et al. 2006; Rothbart and Lewis 1988; Rothbart and Taylor 1992; Tajfel and Turner 1979).

But this level of explanation, while certainly compelling, is only *one* level of explanation, the other being the “ultimate” or “evolutionary” processes that selected for such proximate mechanisms through very long periods of time, and a complete explanation of behavior should thus consider both causal processes. Here we focus on the latter: *How could emotional and cognitive responses that support “heroism” in modern times have been positively selected during humans’ ancestral past?* By definition, heroism involves a fitness cost to the individual (via increased risk of death); hence we might expect it to be selected against, eventually disappearing from the human population. Yet heroism certainly does happen with some frequency across a wide variety of cultures and societies, suggesting that it is a species typical trait. How could this have come to be?

One standard answer is Hamilton’s (1964) famous explanation of how altruism *in general* might have evolved. Hamilton turned attention to the selective fate of genes rather than of individuals per se, pointing out how sacrificial action by one individual *could* result in genes supporting that act spreading more rapidly than had the individual acted selfishly—as long as the beneficiaries of such action were appropriately close relatives.¹ Inclusive fitness has been invoked by Alexander (1979), Masters (1983), Shaw and Wong (1989), Thayer (2004), van der Dennen (1995) and many others in attempts to understand the genetic basis of humans’ propensity for warfare and, using our term, to heroism.² The general point is that, during humans’ remote ancestral past, groups were most probably comprised largely of quite close kin, making a disposition toward sacrificial action on behalf of the group an attribute that could evolve, despite adaptive costs to the individual per se.

Importantly, this account explains heroism as a product of the same ultimate, selective processes that might produce any other altruistic behaviors. Sharing meat from a hunt, for

example, could be explained as readily as fighting for one's group in a battle with other groups. The account nicely combines a plausible reconstruction of family-based social organization in our ancestral past with a foundational idea in modern evolutionary biology. It is also consistent with the pervasiveness of kinship rhetoric—the “fatherland, “band of brothers” etc.—in modern warfare (Johnson 1987). It is quite plausible that the particular form of altruism that interests us, heroism in defense of one's group, evolved via the combined impact of multiple processes that have been invoked for explaining altruism *in general*—including kin altruism, reciprocity in exchange relationships (Axelrod 1984; Trivers 1971) and multi-level selection (most notably, Sober and Wilson 1998).³

Here we develop the possibility that, even without the impact of kin altruism and reciprocity, heroism could have evolved as a “domain specific” form of altruism in response to warfare in our ancestral past. The idea that human cognitive architecture consists, in substantial part, of functionally specific information processing modules is widely accepted in evolutionary psychology and in cognitive neuroscience more broadly, although scholars differ in arguing for a strong version of modularity (notably Cosmides and Tooby 1994; Hirschfeld and Gelman 1994; Sperber 1994) or for a combination of specialized modules and some more general functionality (notably Buller 2005; Fodor 2000; Mithen 1996). The standard strong modularity argument 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.

However this argument plays itself out (for a constructive appraisal see Barrett and Kurzban 2006), the extensive literature on human altruism has, to our knowledge, focused exclusively on the problem of how a *generalized* disposition to altruistic behavior might have evolved. The possibility that multiple, domain specific altruistic dispositions might have evolved independently, each in response to a distinctive adaptive problem and each producing, therefore, at least somewhat different proximate mechanisms, appears to have been overlooked. Since heroism is, by our definition, an altruistic response on behalf of one's group in the event of war with some other group, its task demands would appear *prima facie* quite distinct from those of other altruistic behaviors (e.g., providing food to others and caring for the sick). This makes it plausible that heroism could have evolved on its own trajectory, independent of other forms of altruism, and with warfare as the agent of selection.⁴

Warfare is a group-level phenomenon, and its broad outcomes (victory, defeat, and standoff) are also group-level phenomena. Accordingly, all group members—those who fight as well as those who do not—can suffer “genetic death” should the group be defeated. However, the consequences of group-level outcomes can differ among the individuals comprising such groups. Most important in the present context, those who fight in the group's wars run an increased risk of dying, reducing the probability that their genes will pass on to the next generation. Should the group be victorious, survivors stand to benefit significantly, but heroes are less likely to be among those survivors. Along with 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 for individuals in the warring groups.⁵ 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* ancestral war? Attempts to answer this question have provoked a good deal of controversy. Some accounts of the archeological record suggest that war during humans' evolutionary past was frequent and consequential. Keeley (1997, p. 93), for example, 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.)

In a book that covers much the same territory, LeBlanc (2003, pp. xii - xiii) comments:

Just how common was warfare in the past? I have finally concluded that warfare was quite common... 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.)

Other authors have developed the same general theme (e.g., Bowles 2006; Carman and Harding 1999; Gat 1999; Gat 2006; Martin and Frayer 1997; Rice and 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 at least to our common ancestor with chimpanzees. (See also Alexander 1979; Low 1993; Wilson and Wrangham 2003; Wrangham 1999a; Wrangham and Peterson 1996.)

Why was warfare such an important part of humans' ancestral life? The most plausible explanation invokes humans' achievement of ecological dominance—their becoming the top predator, presumably associated with tool use—making the behavior of other humans the main selective pressure on the species. The argument, first developed by Alexander (1989; 1990), is succinctly stated by Geary (2005 p. 7):

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.

While Geary and others (see also Flinn, Geary, and Ward 2005) build from this assumption to develop the thesis that humans' cognitive capacities are *in general* based on the peculiar demands of social and ecological competition, our concern is more narrowly with the consequences of between-group competition for selection on whatever genes support the single behavior *heroism in war*.

Some anthropologists do challenge the idea that war was a persistent feature of our ancestral past. Fry (2006), for example, takes issue with Keeley and LeBlanc whose books, 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” among humans; he emphasizes “the human potential for peace” as an alternative perspective (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. Nevertheless, few scholars dispute that warfare—or, more broadly, “coalitional violence”—has been present, at least to some extent, throughout our ancestral past, and our question is whether warfare, happening with *any* significant frequency, could have selected for heroism. The simulations that we will now describe (and the analytic section to follow) 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, promoting two behaviors: (1) *communitarianism*—a privately costly but group-benefiting behavior that increases the mean fitness of group members but does not involve fighting external enemies; and (2) *heroism* a privately costly behavior that benefits the group by contributing to the group's success in warfare. In the second simulation, these two behaviors are promoted by two domain specific attributes that are free to evolve independently. A formal description of the two simulations can be found in Appendix 1 which is available on the *Journal's* website; here we provide a verbal account of the two simulations' key features.

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, thus for survival and reproduction. The size of the resource base for each group is a parameter; it can vary across groups but not across time and 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, both as a function of that individual's 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, thus of reproducing) 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 a group can support its members is to capture the resources held by another group. Target groups are chosen at random, with any group that is attacked by another *having* to defend itself by fighting.

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. We will report our simulation findings from the strong assumption that *all* are killed, so that defeated groups are eliminated from the evolving population. While this extreme assumption is certainly consistent with some examples from the historical record (Potidaea, Mytilene, and Melos in the Peloponnesian war, for example), the proportion of a defeated group that is killed is an important parameter, to which we will return later in a later analytic section (a full development is available on the *Journal’s* website). 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 on that attribute. As noted, members of each group vary in altruism at the start of the simulation. During reproduction, variation is maintained by two mechanisms. One models random mutation (defined as M_1 in the appendix on the *Journal’s* website); by default, it occurs here in less than one percent of offspring, and can result in the offspring having an altruism level quite different from the parent. The other mechanism (defined as M_2 in the

appendix) 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 general structure, except that each individual now has 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.

An Aside on Simplicity vs. Realism

Model building necessarily involves reducing the known complexity of the natural world in the interests of simplicity, tractability, and interpretable results. The two models described make a number of simplifying assumptions. Most notably, perhaps, we have not incorporated males' efforts to capture female reproductive capacities as a basis for warfare. As Trivers (1972) classically pointed out, female reproductive capacities are, for males, a critical but scarce resource, one that can be seen as a root cause of male-on-male fighting. Chagnon's (1988) well-known field work among the Yanomamö, for example, supports that position, and the point has been developed recently in the case of civil war by Kanazawa (2006). At the very least, there must have been a complex relationship between capturing somatic resources and capturing females in motivating our (male) ancestors to go to war. Indeed, how such complexity was worked out by the early Israelites is suggested by Betzig (2005, p. 335) in her analysis of the Biblical case (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.

In the same vein, neither of our models explicitly differentiates between males and females. Although our algorithm for reproduction simulates the variability that sexual reproduction entails, offspring have a single parent, and given the strongly sex-typed role of war-fighting, that single parent is most reasonably interpreted as male. While we wish to emphasize that our interest is in *heroism*—risking one’s life on behalf of the group during warfare—and not in *aggressiveness* per se, it is certainly true that, historically, been an overwhelmingly male activity, one that is closely associated with males’ relatively greater propensity to violence (Daly and Wilson 1988). The greater participation of women in war in recent times certainly indicates that women, like men, are quite capable of heroism in warfare, but the available archaeological and anthropological evidence provides much less support for supposing that participation in warfare provided strong selection on women’s heroism as we model that attribute here.

Many other considerations of interest in the study of war are also missing here. When population growth begins to pressure the carrying capacity of a group’s resource base, the model incorporates no internal conflict over the increasingly scarce resources (Diamond 2005), and populations do not have the option of migrating to a different, unoccupied, resource base. When one side wins a war, casualties among the victorious group are modeled only indirectly, via the

reproductive costs suffered in proportion to an agent's heroism. In the simulations—although not, as we will show, in our analytic development—the losing group is completely wiped out.⁶ Groups do not have the option of coalescing with other groups to improve their odds of winning a war or the option of rationally calculating which other group they will attack with an eye to maximizing the probability of victory. Nor does our model incorporate the “security dilemma” that Gat (2000a; 2000b; 2006) has so importantly developed in prisoner's dilemma terms as a reason for pre-emptive fighting. And so on.

In general, however, for this preliminary analysis little is to be gained by developing these complexities. The virtue of focusing on a single causal chain is that if selection on a particular attribute is demonstrated the antecedent of that attribute is clear; but results become increasingly difficult to interpret as further processes are incorporated. The most obvious example is the model's assumption that somatic resources were the critical “limiting factor” underlying our ancestors' going to war with each other. This assumption is consistent with the work of many anthropologists, biologists, ethologists, political scientists, psychologists, sociologists and others addressing the causes of ancient warfare (e.g. Alcock 1978; Carneiro 1970; Durham 1976; Eibl-Eibesfeldt 1979; Kennett et al. 2006; Kennett and Kennett 2000; Kennett and Kennett 2006; Lambert 1997; Lambert and Walker 1991; Shaw and Wong 1989; Thayer 2004; van den Berghe 1978; Wilson and Wrangham 2003). Nevertheless, we acknowledge, with Gat (2006), that somatic resources and males' sexual access to females are both critical, adaptively relevant scarce resources, thus that competition over *both* must have been at the root of ancient warfare. Our models are designed to discover whether heroic propensities could plausibly have been selected for by war even without this additional factor in play.

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 randomly⁷ 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 the group's members from an individual's communitarianism (P_c);
4. The cost to the individual agent of its own communitarianism (C_c);
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 (four).

Each of the 10,000 simulations was run for 1100 generations, allowing a sufficient number of generations for the system to evolve away from diverse starting values. For the last 100 generations we recorded the moving average of *altruism* in the domain general model, and of *communitarianism* and *heroism* in the domain specific model. The simulation parameters (which varied across runs as described above) and the frequency of wars across all generations (an emergent variable) were also recorded for each simulation. In a 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 results.

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 of the 10,000 simulations 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 via its communitarian activities *and* a .25 probability of fighting heroically in any war.

Despite the fact that both behavioral consequences of general purpose altruism are reproductively costly to individuals, therefore, we do observe some positive 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 that individuals reap from their group's success in warfare. Multiple regression of ending altruism values on parameters in the model (see Appendix II on the *Journal's* website) 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. This suggests that higher (and less typical) evolved values of altruism occurred in simulation runs

where the personal cost of altruism was low, where groups were smaller and more equal in size, and where wars were quite 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% respectively and medians of 70.3 and 22.6 respectively; (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; second, that there was 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. We will address the evolution of general purpose altruism shortly; first we discuss the relative evolution of the two domain specific forms.

Why does heroism evolve to higher levels than communitarianism?

In our model heroism is only costly in the event of war. Given that war only occurs periodically—in the simulations any given group goes to war with a probability of about .5 per generation—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 its cost is paid every generation rather than per war. With the mean of this distribution now at .475 (as opposed to .669 in the original domain specific model), clearly this cost difference accounts for some of the relatively greater selection on heroism. Across the range of

parameters, it appears that selection on heroism is stronger when such behavior is not invoked every generation, as is communitarianism. But that is *only* part of the story, since the mean of heroism is still substantially higher when it is evoked every generation than is the mean of communitarianism (.305) when it, too, is evoked every generation.

Another part of the story concerns the immediacy of the military benefits 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*. The delayed effect of communitarianism is, of course, 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 “double-edged sword” for a group. While larger groups are more likely to win wars, high population growth can also be responsible for getting a group *into* war in the first place (faster population growth, produced by communitarianism, means that a group reaches its carrying capacity more rapidly). War always entails some chance of defeat, thus of selection *against* communitarianism. Heroism, on the other hand, is an unambiguous good. In the absence of war, it does no harm to the individual or the group, but in the event of war it *can* be decisive for victory.

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—thus

to the individual's own survival and reproduction—and while both contributions *might* be critical for the outcome of a given war, 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 further than general-purpose altruism?

When heroism and communitarianism are free to evolve independently, both evolve to higher levels than the single, general purpose altruism.⁸ Why is this?

The most straightforward explanation has to do with the more favorable cost-benefit ratio for the specialized behaviors. 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 B, and vice versa. The general purpose capacity will, in other words, pay a cost whenever *either* of the two behaviors is invoked. Conversely, when distinct, special purpose mechanisms are dedicated to A and to 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 that the evolution of one attribute is not handicapped by the cost of the other. Notice that heroism, invoked only every second generation or so, benefits more from such “de-linking of costs” than communitarianism.

This finding points to the cost-benefit logic that could support a modular design for the evolved “cognitive architecture of altruism.” The degree to which propensities for different forms of altruistic behavior are, in modern humans, actually correlated (positively or negatively) is, of course, an empirical question awaiting investigation by other means than computational modeling. Also, findings from the model do not resolve the general problem of how privately costly altruistic dispositions (whether unitary or multiple) actually *did* evolve—a problem that is, of course, much discussed (notably, in recent years, by reference to 'altruistic punishment'; see, e.g. Fehr and Gächter 2002; Fehr and Henrich 2003). Each disposition must still be positively selected despite the costs that it generates for the acting individual. Nevertheless, the finding does raise the possibility that thinking about altruism as a bundle of special purpose forms of altruistic 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. Whatever they might be, selective pressures favoring special purpose *altruisms* (plural) would not have to be as strong, *ceteris paribus*, to overcome the associated costs as would selective pressures favoring general purpose *altruism* (singular) for the behavior in question to evolve.

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 actually was in our ancestral past. Those arguments—and related arguments about the lethality of such warfare—remain for archeologists to resolve. However, as shown on-line in Appendix II, in our simulation the frequency of warfare *does* positively predict selection on altruism in the first model, and selection on both communitarianism and heroism in the second one.⁹

One strong assumption of both simulations is that all members of defeated groups are killed. To examine what happens when this is relaxed, we turned to an analytic model.

An Analytic Model of Heroism

Although, as discussed, our simulations make a range of simplifying assumptions, they are still more complex than what can be readily modeled analytically. Accordingly, we employed a simplified analytic model to explore more rigorously the impact of a few key parameters on the evolution of heroism.¹⁰ 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. (Appendix III on the *Journal's* website contains 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. Although the archeological record does suggest that genocide was at least sometimes practiced in the ancestral past (Keeley 1997; LeBlanc and Register 2003) and the elimination of a competing group has been documented in a chimpanzee population (Wilson and Wrangham 2003), we simply do not know just *how* pervasive this actual outcome was. What happens when the simulation's genocide 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 two 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 were 1.0 and the entire defeated group is to be killed, then an individual hero's actions *would be* critical if the two warring groups were otherwise equal in their summed heroism scores—critical not only

for the group's survival, and hence also for the survival of hero (and thus his chances for reproductive success). At the other extreme with the genocide parameter at zero, all individuals survive the war despite their defeat, meaning that a hero's action, while costing him personally, does nothing to promote the relative survival of his group (including his offspring) compared to the competing group. It follows, therefore, that as G increases, the probability of an individual's heroism rebounding to his own advantage also increases. Figure 4 shows the proportion of heroes q^* as a function of the G parameter across three different population sizes¹¹ when, in equilibrium, it is equally beneficial to be a hero or a coward. (See Proposition 3 and related proof in Appendix III on the *Journal's* website.) As population size increases from 50 through 100 to 200, the slopes of the curves flatten out and the equilibrium proportion of heroes for a given level of the genocide parameter is reduced.

In summary, selection on heroism in the context of warfare is governed by two parameters, genocide and group size: (1) The larger the proportion of the defeated group that is killed, the more critical a hero's action likely will be for his own survival and reproduction, thus for selection on heroism; (2) The smaller the group, the more likely it is that any given individual's heroic action will be critical to the group's survival, thus again for his own survival and reproductive success, hence for selection on heroism.

Summary and Conclusions

Using simulation, we have demonstrated 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 based on the selective pressures of war within a population of groups that, at least sometimes, go to war with each other over scarce resources needed for individual and

group survival. In the first simulation agents are characterized by a general purpose *altruism* (supporting both “communitarianism” and “heroism”) and there is modest positive selection on that attribute. When agents are characterized by the two independent, special purpose attributes *heroism* and *communitarian*, however, both of those attributes evolve to higher levels than general purpose altruism, with heroism evolving to substantially higher levels than communitarianism. All three attributes evolve insofar as the individual’s action, while personally costly, *can* increase the possibility of the group surviving a war, therefore of the individual’s *also* surviving—thus of reproducing.

We have also shown that heroism is particularly likely to evolve when group size is small and when the casualty rate for defeated groups is high. The ecological validity of the first of these parameters is, of course, compatible with the accepted fact that our remote ancestors did live in quite small groups (Dunbar 1993; Dunbar 1996), but the second is more problematic. On the one hand, had we modeled the capture of reproductively valuable females, this would reduce the death rates of defeated groups, increase the growth rate of the victorious group, and allow direct gene flow between defeated and winning groups. On the other, the probability of most or all members of a defeated group being wiped out would, surely, have been higher in small groups than in larger ones.

This said, the analytic model does demonstrate that complete genocide is not necessary for heroism to evolve. It can still do so—albeit, to lower (and we expect, more realistic) levels—with substantially less draconian outcomes to warfare.

Our findings with respect to the possible impact of war on heroism are not incompatible with heroism also evolving in response to Hamiltonian (1964) inclusive fitness. Heroism certainly could have evolved among (small) kinship groups in which members fought in

response to threats to their kin, and it's also likely that the sense of group identity—whether among small units of soldiers or among the millions of those who comprise a modern nation—has its roots in ancient kinship responses. But our results suggest that heroism could also have evolved as a consequence of ancient warfare even *absent* close kinship among groups' members. In fact, attention to the proximate mechanisms we sketched at the outset suggests a complex interaction among the respective mechanisms. On the one hand, if kinship in ancestral times was the sole evolutionary basis for heroism, we would expect modern humans to be less easily persuaded by mere kinship rhetoric to risk their lives for non-kin in large-scale modern wars than they are (Johnson 1987). On the other, if the processes we have identified were all that mattered, we would expect such kinship rhetoric to be irrelevant—which it is not. Clearly, further research is needed on the relative contribution of these two selective forces, and the way in which they might interact in natural circumstances.

Does our model “take the heroism out of heroism” (cf. Trivers 1971)? At the ultimate level at which we are working, it does. This can be seen by considering the extreme case where group size is reduced to one (the acting individual) and the genocide parameter is set at 1. Here the individual is unambiguously fighting *solely* for his own life. While increasing group size beyond that minimum does produce other beneficiaries from the individual's fighting, selection still happens on heroism only to the extent that an individual's heroism is critical for his own survival—and thus can offset the reproductive costs the hero must pay relative to other group members who benefit from his action without having to pay such costs.

But, no doubt, most heroes are responding to particular emotions and cognitive processes, not running such “private fitness accounting equations” in their heads. Hector in front of Troy, for example, *could* have been motivated by knowing that only he had any chance of defeating

Achilles and, therefore, of saving his own life. But there is nothing of that in *The Iliad*. On the contrary, the story makes it clear that he was responding not only to fear for his own life—which he clearly does experience—but to his love of Troy, loyalty to his comrades, honor and, perhaps in the end, to overconfidence that led him to think he *did* have a chance of defeating Achilles. It is his response to those proximate emotions and beliefs that justifies his status as a hero, not the evolutionary logic that, over thousands of previous generations, led him to experience and act on those things in his particular, unfortunate circumstances.

Our finding that communitarianism and heroism, when modeled as separate, domain specific attributes, both evolve to higher levels than domain general altruism has, we believe, implications for research addressing the evolutionary roots of altruistic behavior *in general*. It does not mean that the standard problem of “compensating” altruism for the private costs individuals incur in performing altruistic acts is resolved. Models of how domain-specific, special purpose altruistic dispositions might evolve must still respond to that problem—as, indeed, our model has for heroism and communitarianism. Nevertheless, to the extent that altruisms (plural) will evolve to higher levels when their costs are decoupled, we would expect natural selection to favor such decouplings, thus a quite complex, modular, structure of altruisms (plural) within human’s cognitive and emotional architecture, each responsive to perhaps quite specialized circumstances.

How far such decoupling might proceed would depend, of course, on the particular design efficiencies to be gained by decoupling, and we might expect at least some limits in this respect as well as complementarities at the proximate level (and, presumably, also at the neural level). In general, however, our findings suggest that empirical research might profitably turn attention toward identifying how different forms of altruism evolve differently across different

domains—a move that, once again, will surely be more successful if conducted with an explicit sensitivity to both ultimate and proximate causation.

If the propensity for heroism in warfare is, indeed, a species typical attribute of humans, as our findings suggest is possible, does that condemn us to a future of “constant battles”? Our model does not address that question. In that model, war is triggered by resource stress, but that is an assumption (plausible, we believe, in light of the archeological studies cited earlier), not a finding. An answer to the question, then, depends on the particular proximate emotions and cognitive processes that provoke heroic action in the here-and-now, and whether those could, in themselves, also provoke warfare—not only among our ancestors, but also among ourselves and our descendants.

ENDNOTES

¹ Hamilton's rule is that altruism can evolve 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.

² The list includes Sir R. A. Fisher who, in his foundational work *The Genetical Theory of Natural Selection* (1930, p. 163), addressed the problem of "heroism" in tribal societies finding a solution in terms that anticipated Hamilton's relatedness-based theory of altruism.

³ Various authors have discussed the ways in which mechanisms that have been presented as conceptually distinct might be subsumed by one another. For example: Sober and Wilson (1998) see kin selection as being subsumed by multi-level selection; Reeve (2000) sees Sober and Wilson's model as a special case of Hamilton's equations; and Humphrey (1997) sees kin selection and reciprocity as generalizing into a single broad principle.

⁴ Although the group-level event warfare is the *agent* of selection, we emphasize that the target of selection *per se* is the individual behavior heroism, and by extension whatever configuration of genes might support the propensity to behave heroically. We realize, of course, that the term "heroism" is commonly used more broadly. Becker and Eagly (2004), for example, examine "heroism" exhibited by Carnegie medalists, by non-Jews who risked their lives to rescue Jews during the Holocaust, by kidney donors, and by volunteers for the Peace Corps and Doctors of the World. Here we restrict the term only to altruistic action in warfare.

⁵ 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 (1999); a foundational work on multi-level selection in general is Sober and Wilson (1998). For critical assessments of multi-level selection, see Reeve (2000) and Maynard Smith (1998). In the model to be developed here, groups can live or die as a consequence of warfare, but individual attributes are what replicate, with the individual's behavior *potentially* being critical for the success and survival of the group, thus for replication of his own attributes.

⁶ This simplification was necessary to prevent the population growing out of control, which both expanded groups beyond plausible sizes for ancestral groups and also increased computational demands exponentially.

⁷ From a multivariate uniform distribution with an identity correlation matrix with

$R_g \sim U[50,100]$, $P_b \sim U[0,0.5]$, $P_c \sim U[0,0.5]$, $c_c \sim U[0,0.1]$, $c_H \sim U[0,0.1]$, $S_A \sim U[0,1]$ (S_C , S_H for the two attribute model), $M_1 \sim U[0,0.005]$, $M_2 \sim U[0,0.05]$. Notations specified here

are employed in the formal statement on the *Journal's* website.

⁸ Mean evolved communitarianism and heroism values have a zero correlation. Hence there was no tendency for something akin to generalized altruism to evolve in the second, domain specific model; nor was there evidence for agents to “specialize” in a particular form of domain-specific altruism.

⁹ Other key input parameters such as the cost of heroism, the size of groups' resource bases, and variation in the size of groups' resource bases were all significant *negative* predictors of heroism.

¹⁰ In our simulation, genocide in the event of defeat is the only way that agents die. Reducing the level of genocide in the simulation produced exponential population growth and constant war—along with a vastly increased demand on computational resources. With $G = 1$, however, population size remains more or less constant, cycling around the same mean. Accordingly, for the analysis of genocide and population size, we have relied exclusively on the analytic results.

¹¹ In the analytical model with the total population consisting of two groups, 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.

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Figure 1.

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

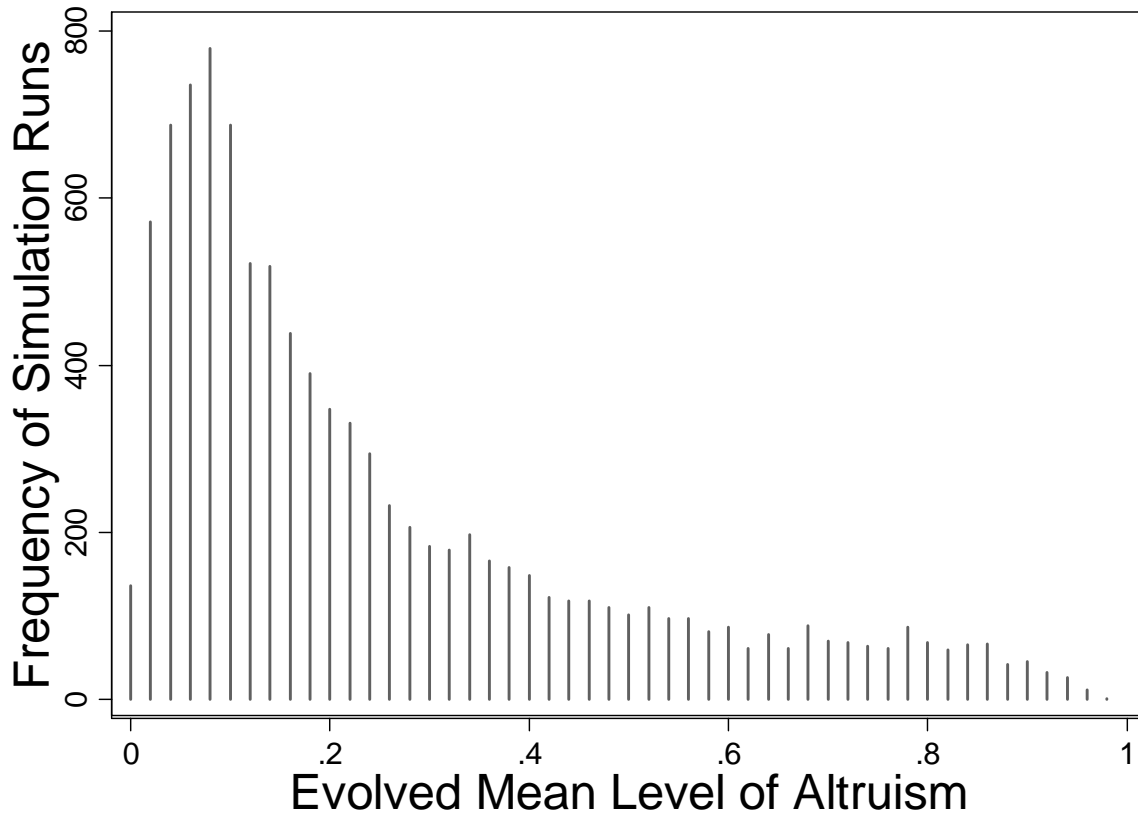


Figure 2a.

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

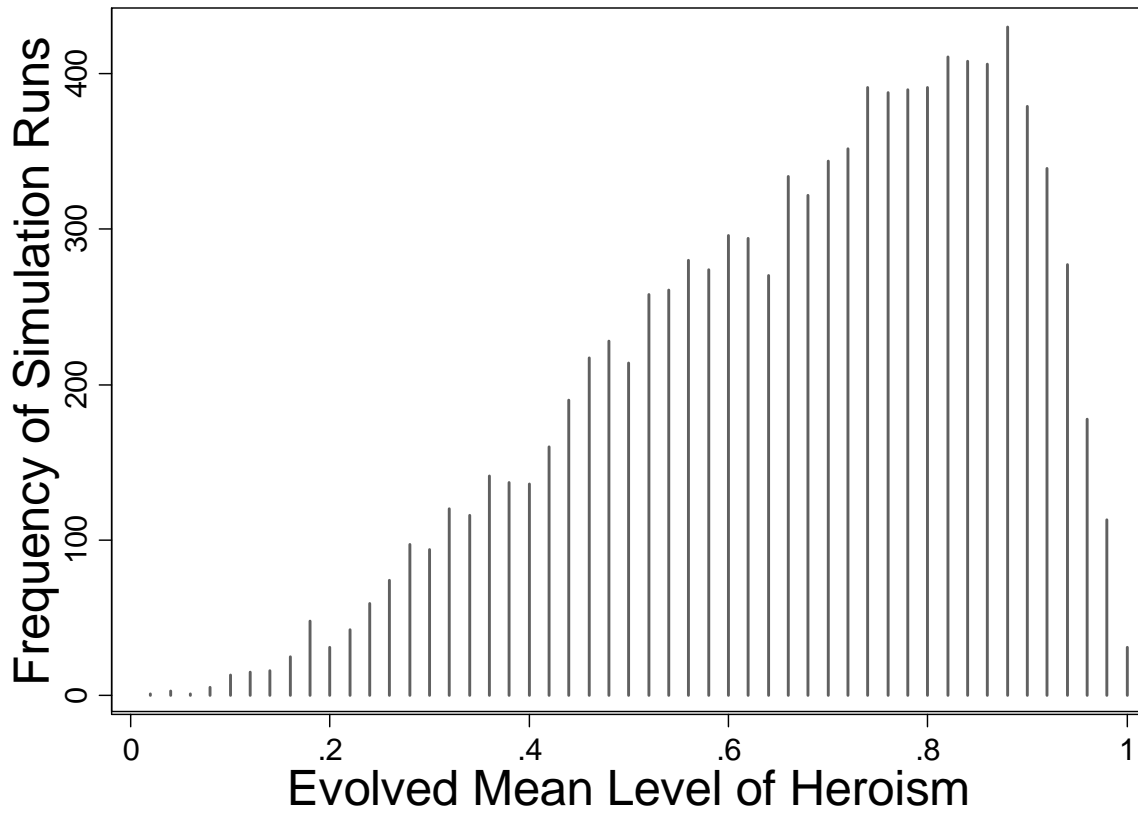


Figure 2b.

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

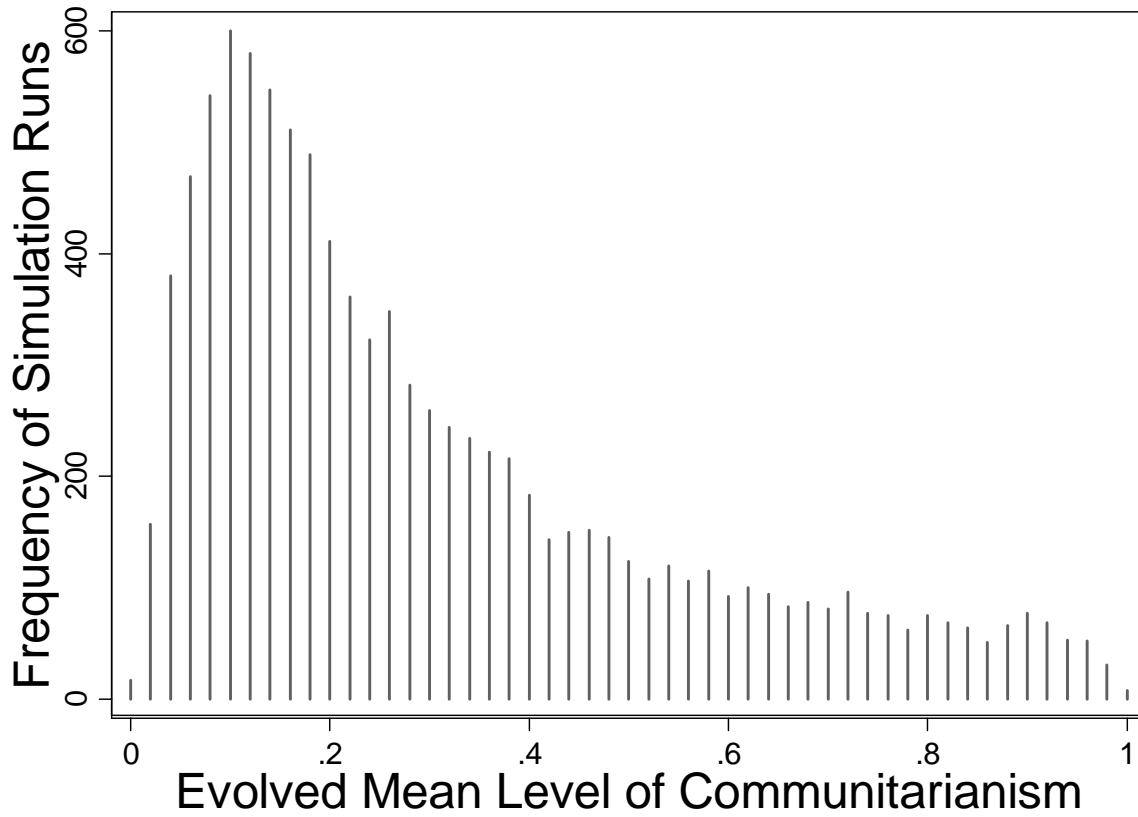


Figure 3.

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

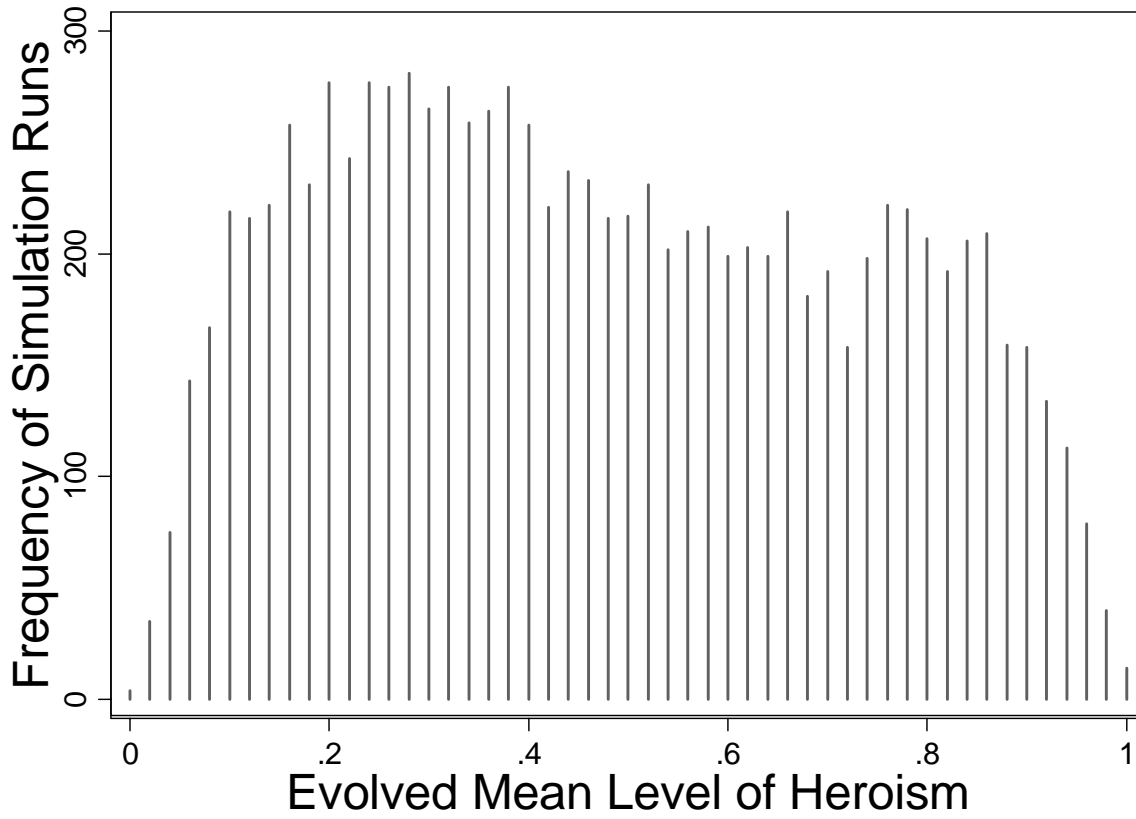


Figure 4.

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

