Did Warfare among Ancestral Hunter-gatherers Affect the Evolution of Human Social Behaviors?

Samuel Bowles
9 April, 2009

Since Darwin, inter-group hostilities have figured prominently in explanations of the evolution of human social behavior. Yet whether ancestral humans were largely “peaceful” or “warlike” remains controversial. I ask a more precise question: if more cooperative groups were more likely to prevail in conflicts with other groups, was the level of inter-group violence sufficient to exert a significant influence on the evolution of human social behavior? Using a model of the evolutionary impact of between-group competition and a new data set that combines archaeological evidence on causes of death during the Late Pleistocene and early Holocene with ethnographic and historical reports on hunter-gatherer populations, I find that the estimated level of mortality in inter-group conflicts would have had significant effects, allowing the proliferation of group-beneficial behaviors that were quite costly to the individual altruist.
**Introduction**

Inter-group hostilities figure prominently in a number of explanations of the evolution of human social behavior, starting with Darwin (1). The underlying mechanism is that (as Darwin put it) groups with “a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other... would spread and be victorious over other tribes” (1):156. An implication is that if intergroup conflict is frequent and lethal, then more altruistic group-beneficial behaviors -- those entailing greater costs to the individual altruist -- will be able to proliferate.

Notwithstanding a number of insightful recent studies, however (2-4), lethal inter-group conflict among hunter-gatherers during the Late Pleistocene and early Holocene remains a controversial subject, with little agreement on either its extent or consequences (5, 6). Among the empirical challenges are the lack of written accounts, the difficulty in making inferences from hunter-gatherers in the ethnographic record about conditions before the domestication of plants and animals and the emergence of states, and the fact that most foragers made little use of fortifications and killed each other with the same weapons that they used to hunt other animals, thus leaving few distinctive archeological traces other than skeletal remains.

In light of the available archaeological and ethnographic evidence, could war among ancestral humans have had substantial effects on the evolution of altruistic behavior? To answer the question I draw upon recent models of human evolution in which competition between groups plays a prominent role (7-14) to allow a quantitative assessment of the relationship between the frequency and intensity of warfare and the selective pressures operating on altruistic behaviors. I use a variant of these models along with a new set of empirical estimates of the extent of war among both pre-historic and historic hunter-gatherers to derive an explicit measure
of the importance of warfare in the evolution of human social behavior. This measure is the maximum degree of altruistic behavior — namely $c^*$, the greatest cost borne by individuals in order to benefit fellow group members — that could have proliferated given the empirically likely extent of warfare during the Pleistocene and early Holocene.

The virtual absence of archaeological evidence of persistent economic and political differentiation between families prior to about fourteen thousand years ago (15) indicates that the most informative data for understanding Late Pleistocene and early Holocene humans pertain to hunting and gathering populations without formal political structures (chiefs, big men, or states). I exclude populations making substantial use of domesticated plants and animals, namely, pastoral, horticultural, agricultural or equestrian hunting populations. As hunter-gatherer populations occupying resource-rich areas in the Late Pleistocene and early Holocene were probably sedentary (at least seasonally), I have included wars involving settled as well as purely mobile populations.

By ‘wars’ I mean events in which coalitions of members of a group seek to inflict bodily harm on one or more members of another group. The term is not ideal for the ambushes, revenge murders, and other kinds of hostilities likely to have occurred between ancestral groups of humans. Most hostile inter-group contact among hunter-gatherers was probably ongoing or intermittent, with occasional casualties, more akin to boundary conflicts among chimpanzees (16) than to the pitched battles of modern warfare.

Using these definitions and selection criteria, I studied all available archaeological and ethnographic sources that present (or are cited as presenting) relevant data. Of these 34 sources, 14 were found to present data that was unrepresentative (for example when warfare was primarily with modern agricultural populations), unreliable, or inadequate. In three cases re-
estimation of the critical information was possible. Skeletal evidence from sites with fewer than 10 individuals was also excluded. Possible biases in this data set are discussed below. The 8 ethnographic and 15 archaeological included sources yield similar results (Table 1) consistent with the view that prehistoric warfare was frequent and lethal, but somewhat less so than estimates based on data in the standard source for these estimates (6). The populations studied appear in Figure 1. (Details and additional caveats these and the data to follow appear in (17).)

Inter-group conflict and the evolution of social behaviors

While both genetic and cultural transmission is almost certainly involved in the evolution of altruistic behaviors, I model only the former, not because it is more important but because it presents greater challenges. (I comment on extensions to cultural transmission below).

The primary behaviors thought to have been spread by war are what Darwin termed the ‘social and moral qualities’ and other forms of altruism. This paradoxical role of war arises because, in the absence of within-group positive assortment, altruism will be suffer adverse within-group selection, but might be sustained by the between-group selection pressures that warfare introduces if altruists willingly fight on behalf of others in their group so that otherwise comparable groups with many altruists tend to prevail in inter-group contests. In game theoretic terms, defense or predation is a public good (an n-person Prisoner’s Dilemma) in which those who participate confer benefits on their fellow group members at a cost to themselves. While I treat the case of the altruist as warrior as paradigmatic, willingness to take mortal risks as a fighter is not the only form of altruism that contributes to prevailing in intergroup contests; more altruistic and hence more cooperative groups may be more productive and sustain healthier, stronger, or more numerous members, for example, or make more effective use of information.
The two key determinants of the effect of warfare on the evolution of social behaviors are the extent of genetic differences between the winners and losers of conflicts and the effect of the number of altruists in a group on group members’ average fitness. Warfare affects the second by making the presence of altruists in a group critical to the members’ survival (and hence their fitness). There are two ways that the outcome of a conflict may affect the average fitness of its members. The first is that members of losing groups are more likely to perish and those who die may either produce no offspring or leave children who suffer high mortality due to inadequate parental care. The second is that, as in chimpanzees (18), weaker groups cede territory, thereby redistributing fitness-relevant resources between the groups.

I consider a large population made up of a number of sub-populations which periodically engage in hostile contests and study an altruistic behavior that is costly to the individual and has no beneficial effects for group members other than increasing the group’s probability of prevailing in inter-group contests. Groups are sufficiently large that the increased probability of group success in conflict that is associated with an additional altruistic member does not compensate the individual for the cost of the behavior in question. Thus adopting the altruistic behavior decreases the expected fitness of an individual (by comparison to an individual eschewing the behavior) while increasing the expected fitness of other group members (19). For simplicity, I represent the altruistic behavior in question as the expression of a single allele and let individuals reproduce asexually; the model is readily extended to any form of vertical transmission, including cultural.

**Modeling warfare and conditions under which altruism may evolve**

Following (12) suppose that in every generation with probability $\kappa$ a group is paired for a contest with another group and survives with probability $\lambda$, which is increasing in the fraction of
altruists in the group. Groups are the same size (normalized to 1) except that groups that have
won a contest are momentarily of size 2 (the other group is eliminated). The surviving group
divides, forming two daughter groups of equal size. The size of group j next generation is thus 1,
2 or 0 with probabilities \((1-\kappa), \kappa\lambda, \text{ and } \kappa(1-\lambda)\), respectively, so expected size is \(w_j = 1-\kappa + 2\kappa\lambda\).
The effect of the prevalence of altruists on the expected size of the group next generation is the
likelihood of a contest \((\kappa)\), times the effect on group size of surviving or not \((2)\), times the effect
of the prevalence of altruists on the probability of a group surviving should a contest occur \((\lambda_A)\),
that is: \(\kappa 2\lambda_A\).

Let \(p_{ij} = 1\) if individual i in group j is an altruist with \(p_{ij} = 0\) otherwise. Let \(p_j\) be the
fraction of group j’s membership that are altruists, \(p\) and \(p’\) be the altruist-fraction of the meta-
population in a given and subsequent generation, respectively, and \(\Delta p = p’ - p\). Then using the
Price equation \((20)\) and assuming a constant meta-population size, the evolution of altruism
(summarized by \(\Delta p\)) can be expressed as a between-group effect plus a within-group effect:
\[
\Delta p = \text{var}(p_j)\beta_G + E\{\text{var}(p_{ij})\}\beta_i
\]
The terms \(\text{var}(p_j)\) and \(E\{\text{var}(p_{ij})\}\) respectively are the between-group and within-group genetic
variance. \((E\{\})\) indicates a size-weighted average over groups.) The coefficient \(\beta_G\) is the effect of
variation in \(p_j\) on the average fitness of members of group j \((w_j)\) which (see above) is:
\[
(2) \quad \beta_G \equiv \frac{d w_j}{d p_j} = \kappa 2\lambda_A
\]
The coefficient \(\beta_i\) is the effect of variation in \(p_{ij}\) (namely switching from an non altruist to an
altruist) on the fitness of an individual in group j \((w_{ij})\):
\[
(3) \quad \beta_i \equiv \frac{d w_{ij}}{d p_{ij}} = -c + \kappa 2\lambda_A / n
\]
where \(-c\) is the direct fitness effect of adopting the altruistic behavior and the second term is the
indirect positive effect on the individual’s fitness that results from the group’s greater probability
of prevailing in a contest. This indirect effect is \( (dw_j/dp_j)(dp_j/dp_{ij}) \) and is derived using equation (2) and \( dp_j/dp_{ij} = 1/n \), where \( n \) is group size (number of individuals in a single reproducing generation in the absence of reproductive skew, fluctuations in group size and non-random migration).

Wright’s inbreeding coefficient \( F_{ST} \) is the ratio of between-group to total genetic variance \( \equiv \text{var}(p_j)/\text{var}(p_j) + E\{\text{var}(p_{ij})\} \), so one can rearrange (1) to give a condition for the proliferation of the altruistic trait (namely \( \Delta p > 0 \)):

\[
F_{ST}/(1-F_{ST}) > -\beta_i/\beta_G
\]

which says that the extent of genetic differentiation among groups must be greater than the ratio of the costs of the altruistic behavior (the within-group selection pressure) to the benefits (the between-group selection pressures). Equation (4) is a multi-level selection analogue to Hamilton’s rule \{Hamilton, 1964 #781\} for the proliferation of altruism by kin selection.

With these results, the condition for an altruistic allele to proliferate (4) can be written

\[
F_{ST}/(1-F_{ST}) > c/\kappa \lambda A - 1/n
\]

Rearranging (5), I define the critical value \( c^* \) as the maximum cost of the altruistic behavior consistent with its proliferating in the population:

\[
c^* = \kappa \lambda A \{F_{ST}/(1-F_{ST}) + 1/n\}
\]

To estimate \( c^* \) one needs to know how frequent and how lethal intergroup conflicts were. The richest source is the skeletal evidence studied by archaeologists.

**Archaeological evidence**

As with all archaeological data, it is difficult to establish if the sites that have been studied are representative of Late Pleistocene and early Holocene conditions. As these sites involve burials they are almost certainly not representative in one respect: simple disposal of the
dead (rather than burial) appears to be typical of the archetypal so-called “immediate return” foraging group (21). There may be more than accidental bias in the burials studied for signs of violence, given that evidence of violent deaths may be deemed more interesting or worthy of publication than the absence of such evidence. Evidence on given individuals are also incomplete, leading to the opposite bias. Most skeletal remains are never found, and those that are range from intact to fragmentary or poorly preserved, often comprising just a few of the 100 or so bones in an adult human (setting aside the small bones of the hands and feet). The remains of 2185 pre-historic people of Californian are accessible to researchers in a museum collection that totals only 12,044 bones (excluding hands and feet); more than ninety percent of the individuals’ bones are absent (22).

Moreover, while some osteological evidence is indicative of ongoing inter-group violence (simultaneous burials, severed limbs and other evidence of trophy taking, for example), one cannot always distinguish between deaths due to inter-group violence and that occurring within groups. Other biases may lead to underestimates. Many deaths in warfare do not leave projectile points embedded in bone or the other traces of violent death: “an analysis that included only projectile points embedded in bone would miss over half of the projectiles ... and 75 percent of what was in all probability the actual number of projectile wounds” (23). Studies of arrow wounds treated by U.S. Army surgeons during the Indian Wars found that fewer than a third of the arrows struck bone (24) and that 61 per cent of fatal arrow wounds were to the abdomen (25). Finally, fatalities during combat may fall far short of the total effect of warfare when account is taken of the mortality and reduced reproductive success occasioned by the displacement of the surviving losers. Table 2A gives the resulting estimates.
Ethnographic evidence

Most ethnographic studies of pre-modern war have concerned populations whose unusually bellicose relations among groups may not reflect conditions of Late Pleistocene hunter gatherers: horticultural peoples in the highlands of Papua New Guinea and parts of lowland South America, or equestrian hunters or sedentary horticulturalists in North America. Among non-equestrian foragers, detailed accounts provide examples of inter-group conflict of exceptional brutality among Aboriginal Australians, Eskimos and other groups, but most do not allow quantitative estimates of the resulting mortality. In other groups war is entirely absent from the ethnographic record, but in some of these cases, like the !Kung and other Southern African groups this may be the result of recent state interventions. For 8 populations ethnographic studies allow estimates of the deaths due to warfare as a fraction of total mortality (summarized in Table 2B). As in the case of archaeological studies, selection bias may lead to an exaggeration of the extent of warfare mortality. Moreover, some populations are not entirely representative of foragers during the Late Pleistocene due to the impact of non-hunter-gatherer influences.

Calibrating the model with hunter-gatherer data.

To estimate c* -- the maximal direct individual cost of a group-beneficial behavior that could have proliferated -- I translate our estimated per-generation mortality rates into an equivalent frequency of decisive conflicts in which the entire territory of a group is taken by the winners, and the losing population is eliminated. This allows treatment the territorial losses and mortality in a consistent way, and to maintain a constant group size, greatly simplifying the analysis. The data on mortality provide an estimate of \( \kappa \), the per-generation probability of such a decisive conflict. Mortality results when a group loses a conflict, occurring with probability
\( \kappa (1-\lambda) \). If war does not occur or if the group engages in war but prevails then all deaths are from other causes, so \( \kappa (1-\lambda) \) is estimated by \( \delta \), the fraction of mortality due to war. Averaging across groups, \( \lambda = \frac{1}{2} \); so \( \delta = \frac{1}{2} \kappa \) giving \( \kappa = 2\delta \).

We need two additional pieces of information: the effect of additional altruists on the probability of group survival (\( \lambda_A \)) and the extent of genetic differentiation among groups (\( F_{ST} \)).

There is no way to estimate \( \lambda_A \) empirically for hunter-gatherers, and it may vary depending on the degree of imbalance between the warring groups, the available weapons and the nature of the conflict (ambush, pitched battle) and the terrain (open plains, mountain pass). The intuitive meaning of alternative functions is illustrated in Figure 2. For the contest success functions illustrated, the assumption that the success function is approximately linear (\( \lambda_A \) is a constant) works as long as the groups are not very imbalanced. Because I use a probabilistic (rather than deterministic) function even groups with substantial fractions of altruists on average suffer significant mortality. For example, if the difference between two groups in the fraction of altruists is ten percent and \( \lambda_A = 2 \) then should a conflict occur, the expected mortality of the group with fewer altruists is just 1.50 times the mortality in the more altruistic group (17). (For the mortality in the less altruistic group to be double that of the more altruistic group \( \lambda_A = 3.3 \) would be required.) Even with very frequent conflicts, e.g. \( \kappa = 0.2 \) (and \( \lambda_A = 2 \)) the difference in the expected size (next generation) of these two groups is only 0.04.

Available estimates of \( F_{ST} \) for hunter-gatherer populations measure the extent of genetic differentiation both among subpopulations within a given ethno-linguistic group (e.g. among the !Kung in Botswana) and among subpopulations in more than one ethno-linguistic group (e.g. among 18 ethnic groups in Southern Africa). Because prehistoric warfare probably was most common on the boundaries of an expanding ethno-linguistic unit, the latter measure may be the
more appropriate for this study. Excluding those populations that currently live at such a distance one from another that it is unlikely that they interacted in the distant past and those that are not at least somewhat reproductively isolated from non-hunter-gatherer populations, there is a total of 18 estimates among hunter gather groups \( (17) \). The mean \( F_{ST} \) of the 18 estimates is 0.074, while that for the 15 estimates between ethno-linguistic groups is 0.078. The median for both sets is 0.075. Differences in the genetic material and statistical methods on which these estimates are based make direct comparisons difficult (the Pygmy and Arnhem Land estimates are based on microsatellite data and as a result are likely to be underestimates \( (30, 31) \)). In the illustrative calculations below (Figure 3) I use the median and range of the estimates for between ethno-linguistic group differentiation.

**Results**

I can now answer the question with which I began: what is the maximum cost of altruism \( (c^*) \) such that the group benefits would offset the within-group selection pressures against the altruists? To decide whether the resulting values of \( c^* \) are “large” or “small,” note that \( c^* = 0.03 \) is a quite substantial cost, one that in the absence of inter-group competition would lead the fraction of altruists in a group to fall from 0.9 to 0.1 in just 150 generations. An illustration more directly related to the question of warfare is the following. Suppose that in every generation a group is engaged in a war with probability \( \kappa = 2\delta \) and that an altruistic “warrior” will die with certainty in a lost war and with probability 0.20 in a war in which the group prevails, while non-altruistic members also die with certainty in lost wars but do not die in won wars. (These mortality assumptions are extremely unfavorable for the altruists.) Assuming the altruists have no reproductive advantages during peacetime, then \( c = 0.2\delta \), or (using the mean estimate of \( \delta \) from Table 1) \( c = 0.028 \).
To study the evolutionary consequences of warfare under Pleistocene conditions using recent data one would ideally use estimates of both genetic differentiation and wartime mortality from hunter-gatherer populations living in close proximity with one another but having little contact with farmers or herders. Such groups exist in Arnhem Land, Australia, the continent thought by many to be the best laboratory of likely Pleistocene and early Holocene conditions among foragers (32). Depictions of warriors and battles in the rock art of Arnhem Land populations date from as early as ten thousand years ago (33). The availability of archaeological, ethnographic and genetic data for this region makes it a remarkable laboratory for this investigation.

Table 3 presents data on the extent of wartime mortality in three nearby groups of foragers— the Anbara, Murngin, and Tiwi -- along with estimates of genetic differentiation among seven Aboriginal groups (including the Tiwi and the Murngin) in that relatively small area(34). The estimates of $c^*$ for these populations of (assuming $\lambda_A = 2$) make it clear that if groups were as differentiated as these populations and as warlike as the Murngin, between-group competition could overcome very strong within-group selection against an altruistic behavior. Even for groups similar to the more peaceful Anbara, quite costly forms of altruism could proliferate by this mechanism ($c^* = 0.029$). The second line in the table gives the values of $c^*$ for very large (strictly infinite) groups, that is ignoring the term $1/n$ in equation 6 and thus eliminating the direct benefit accruing to the altruist.

To explore the importance of variations in $\lambda_A$ Figure 3 uses the extreme $F_{ST}$ values for differentiation between ethnolinguistic groups (Native Siberian and Pygmy) and the median of these values (South African) to show the combinations values of $\lambda_A$ and $\delta$ such that the between-group selection would offset a $c^* = 0.03$. Figure 3 indicates that for plausible values of
the effect of altruistic behaviors on a group’s chances of prevailing in contests ($\lambda_A$), the levels of warfare mortality observed in many populations would offset substantial costs of altruism.

**Discussion**

The mortality data summarized in Table 1 are consistent with what is known about the Late Pleistocene from more indirect data. Frequent lethal intergroup encounters may reconcile two otherwise anomalous facts about hunter-gatherer demographics. Human population grew extraordinarily slowly or not at all for the 100,000 years prior to 20,000 years before the present (35, 36), yet under peaceful conditions foraging populations are capable of growth rates in excess of 2 percent per annum (37, 38).

Further, the extraordinary volatility of climate during the Late Pleistocene (39) must have resulted in natural disasters and periodic resource scarcities, known strong predictors of inter-group conflict among hunter-gatherers in the historical record (40), and undoubtedly forced long-distance migrations and occasioned frequent encounters between groups having no established political relations. The mortality data from Southern California (23) and Nubia (41) are consistent with this hypothesis.

The evidence that intergroup conflict may have contributed significantly to the proliferation of a genetically predisposition to behave altruistically does not mean that it did, or that the mechanism I have described explains the evolution of human altruism. The model applies with even greater force to behaviors transmitted culturally rather than genetically, in part because between-group differentiation is considerably greater and hence the evolutionary impact of differential group success in contests is stronger.

One cannot say with certainty which of these data should be the basis for our conclusions concerning the evolutionary impact of lethal intergroup competition during the late Pleistocene
and early Holocene. Even though periods of climatic volatility would bring even quite distant
groups into contact during migrations, the far flung settlements of the circumpolar regions, desert
Southern Africa, and Western Australia, would be far less likely to be in contact – either
conflictual or beneficial – than groups living in closer proximity such as those in coastal Arnhem
Land and lowland New Guinea. Moreover the more populated coastal and riverine areas
contributed disproportionately to the gene pool of subsequent generations. But taking all of the
evidence into account, it seems likely that, for many groups and for substantial periods of human
pre-history, lethal group conflict may have been frequent enough support the proliferation of
quite costly forms of altruism.

This might help explain why altruism often does not extend across group boundaries,
and how this kind of “parochial altruism” may have evolved in humans (13) and perhaps even
other animals. Because humans are far from unique in the extent of lethal inter-group conflicts
(42) and because genetic differentiation among populations of some other “warlike” animals
may not be very different from that among humans (43), there remains the as-yet-unexplored
possibility that a similar evolutionary dynamic may occur in other animals.
Table 1. Fraction of total mortality due to warfare ($\delta$): summary statistics. Note: complete sources, methods and other details for this and Table 2 are in (17). Weights are the square root of the total number of deaths.

<table>
<thead>
<tr>
<th></th>
<th>Weighted mean</th>
<th>Arithmetic Mean</th>
<th>Median</th>
</tr>
</thead>
<tbody>
<tr>
<td>Archaeological</td>
<td>0.12</td>
<td>0.14</td>
<td>0.12</td>
</tr>
<tr>
<td>Ethnographic</td>
<td>0.16</td>
<td>0.14</td>
<td>0.13-0.15</td>
</tr>
<tr>
<td>All</td>
<td>0.14</td>
<td>0.14</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Table 2A. Archaeological evidence on the fraction ($\delta$) of adult mortality due to warfare

Note: before present indicates before 2008

<table>
<thead>
<tr>
<th>A. Archaeological Evidence Site</th>
<th>Approx date (yrs before present)</th>
<th>Author (date)</th>
<th>$\delta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>British Columbia (30 sites)</td>
<td>5500-334</td>
<td>Cybulski (1994)</td>
<td>0.23</td>
</tr>
<tr>
<td>Nubia (site 117)</td>
<td>14-12000</td>
<td>Wendoff (1968)</td>
<td>0.46</td>
</tr>
<tr>
<td>Nubia (near site 117)</td>
<td>14-12000</td>
<td>Wendoff (1968)</td>
<td>0.03</td>
</tr>
<tr>
<td>Vasiliv’ka III, Ukraine</td>
<td>11000</td>
<td>Telegin (1961)</td>
<td>0.21</td>
</tr>
<tr>
<td>Volos’ke, Ukraine</td>
<td>‘Epipalaeolithic’</td>
<td>Danilenko (1955)</td>
<td>0.22</td>
</tr>
<tr>
<td>S. California (28 sites)</td>
<td>5500-628</td>
<td>Lambert (1997)</td>
<td>0.06</td>
</tr>
<tr>
<td>Central California</td>
<td>3500-500</td>
<td>Moratto (1984)</td>
<td>0.05</td>
</tr>
<tr>
<td>Sweden (Skateholm I)</td>
<td>6100</td>
<td>Price (1985)</td>
<td>0.07</td>
</tr>
<tr>
<td>Central California</td>
<td>2415-1773</td>
<td>Andrushko et al (2005)</td>
<td>0.08</td>
</tr>
<tr>
<td>Sarai Nahar Rai, N.India</td>
<td>3140-2854</td>
<td>Sharma (1973)</td>
<td>0.30</td>
</tr>
<tr>
<td>Central California (2 sites)</td>
<td>2240-238</td>
<td>Jurmain (2001)</td>
<td>0.04</td>
</tr>
<tr>
<td>Gobero, Niger</td>
<td>16,000–8200</td>
<td>Sereno et al. (2008)</td>
<td>0.00</td>
</tr>
<tr>
<td>Calumnata, Algeria</td>
<td>8300-7300</td>
<td>Chamla et al (1970)</td>
<td>0.04</td>
</tr>
<tr>
<td>Ile Teviec, France</td>
<td>6600</td>
<td>Newall et al (1979)</td>
<td>0.12</td>
</tr>
<tr>
<td>Bogebakken, Denmark</td>
<td>6300-5800</td>
<td>Newall et al (1979)</td>
<td>0.12</td>
</tr>
</tbody>
</table>
**Table 2B. Ethnographic evidence on the fraction (δ) of adult mortality due to warfare**

*Note a indicates that the group were foragers; b maritime; c seasonal forager-horticulturalists; d, sedentary hunter-gatherers; e, recently settled.*

<table>
<thead>
<tr>
<th>B. Ethnographic evidence</th>
<th>Dates</th>
<th>Author (date)</th>
<th>δ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ache, Eastern Paraguay a</td>
<td>pre-contact (1970)</td>
<td>Hill &amp; Hurtado (1996)</td>
<td>0.30</td>
</tr>
<tr>
<td>Hiwi, Venezuela-Colombia a</td>
<td>pre-contact (1960)</td>
<td>Hill et al. (2007)</td>
<td>0.17</td>
</tr>
<tr>
<td>Murngin, NE Australia ab</td>
<td>1910-1930</td>
<td>Warner (1931)</td>
<td>0.21</td>
</tr>
<tr>
<td>Ayoreo, Bolivia-Paraguay c</td>
<td>1920-1979</td>
<td>Bugos (1985)</td>
<td>0.15</td>
</tr>
<tr>
<td>Tiwi, N. Australia d</td>
<td>1893-1903</td>
<td>Pilling (1968)</td>
<td>0.10</td>
</tr>
<tr>
<td>Modoc, N. California d</td>
<td>‘aboriginal times’</td>
<td>Ray (1963)</td>
<td>0.13</td>
</tr>
<tr>
<td>Casiguran Agta, Philippines a</td>
<td>1936-1950</td>
<td>Headland (1989)</td>
<td>0.05</td>
</tr>
<tr>
<td>Anbara, N. Australia abc</td>
<td>1940-1960</td>
<td>Hiatt (1965)</td>
<td>0.04</td>
</tr>
</tbody>
</table>

**Table 3. Largest cost (c*) for an altruistic trait to proliferate given estimates of genetic differentiation and mortality in inter-group hostilities (δ) among three Arnhem Land Australian hunter gatherer populations.**

*Note: The entries are given by equation (6) where κ = 2δ. Genetic differentiation (F<sub>ST</sub> = 0.040) is among 7 groups (including Tiwi and Murngin (see Figure 3) and is from (34)(see also (17)); δ is from Table 2; λ_A = 2; n = 26 the size of a single generation in a coalition of 3 groups of the census size considered to be typical of non-equestrian, non-Arctic foragers during the Late Pleistocene (44).*

<table>
<thead>
<tr>
<th></th>
<th>Murngin</th>
<th>Tiwi</th>
<th>Anbara</th>
</tr>
</thead>
<tbody>
<tr>
<td>δ = 0.207</td>
<td>0.133</td>
<td>0.064</td>
<td>0.029</td>
</tr>
<tr>
<td>δ = 0.100</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>δ = 0.045</td>
<td>0.064</td>
<td>0.033</td>
<td>0.015</td>
</tr>
</tbody>
</table>

n = 26

n = ∞
Figure 1. Sources of archaeological (black squares) and ethnographic (black closed dots) evidence on warfare and genetic (black open dots) data on between group differences
Figure 2 A. Contest success probabilities \( \lambda^A(p_j, p) = \lambda^A(p_j, \frac{1}{2}) \) for group \( j \) if half of the opposing are altruists. Note: The parameter \( \mu \) determines the slope of the function (namely, \( \lambda_A \)) at \( p_j = 0.5 \). This success function differs from the Lanchester model (45) in which the group with more combatants wins with certainty and the rate of losses of the two groups per unit of time depends on the square of the number of fighters in each. The implied Lanchester model survival function in the figure would be a step function with the step at one half, which would imply much stronger effects of warfare on the evolution of social behavior (8).

Figure 2 B. Wartime mortality (\( \delta \)) and the effect of altruism on success in conflicts (\( \lambda_A \)) sufficient for the proliferation of an altruistic trait with \( c = 0.03 \) for three estimates of the extent of genetic differentiation among groups (\( F_{ST} \)). Note: Shown are the values of \( c^* \) consistent with equation 6 for the estimated F values from (12) (see also (17)). The representative values of \( \delta \) are from Table 2. Populations on the horizontal axis in italics are from the ethnographic sample, the rest are from the archaeological sample.
Figure 3. Data sources in Arnhem Land Australia for ethnographic evidence on warfare (black dots) and genetic differentiation (open dots). Source: Table 2B above and (34) The maximum distance between pairs of groups shown is about 600 kilometers.
The author declares no competing interests. Affiliation: Santa Fe Institute, 1399 Hyde Park Rd, Santa Fe, New Mexico, U.S.A and University of Siena, Siena, Italy.

References and Notes.


46. Thanks to Iren Levina and Alina Vereshchagina for translating the Russian and Ukrainian archaeological materials, Patricia Lambert and Kenneth Kennedy for assistance with the Californian and Indian archaeological evidence, Margaret Alexander, Bruce Bertram, Luca Luigi Cavalli-Sforza, Tim Clutton-Brock, Wayne Cote, Emma Einhorn, Diane Wood Gordon, Hillard Kaplan, Kim Hill, Kristin Howard, Sung Ha Hwang, Kevin Langergraber, Steven Le Blanc, John Mitani, Carolyn Resnicke, Robert Rowthorn, Paul Seabright, Eric Alden Smith, Timothy Taylor, Della Ulibarri, Linda Vigilant, Elisabeth Wood, and Richard Wrangham for valuable contributions, and to the Behavioral Sciences Program of the Santa Fe Institute, the U.S. National Science Foundation, the European Science Foundation and the University of Siena for support of this work.