blunts ectopic HIF-2α–induced increases in hepatic *Epo* gene expression, whereas concomitant Sirt1 and HIF-2α overexpression further augments hepatic *Epo* gene expression in normoxic mice compared with ectopic HIF-2α overexpression alone.

Although Sirt1 overexpression augments HIF-2α–induced *Epo* expression, increased Sirt1 activity alone is not sufficient to induce hepatic *Epo* gene expression in mice. Interestingly, HIF signaling and Sirt1 activity in the liver are inversely regulated during caloric restriction. Whereas caloric restriction of aged rats results in reduced HIF-1 signaling and blunted expression of HIF target genes in the liver, including *Epo* (*38*), caloric restriction is associated with increased hepatic Sirt1 activity (*39*), which indicates that Sirt1 or HIF-2α signaling pathways can be controlled independent of each other in a stress-dependent manner. In addition to repressing HIF-1α signaling, caloric restriction may directly repress HIF signaling induced by HIF-2α. Alternatively, caloric restriction may induce expression of a repressor of *Epo* gene expression that suppresses Sirt1/HIF-2α signaling in a dominant fashion.

Our data integrate Sirt1-HIF-2α signaling with other stress-responsive, prosurvival signal transduction pathways that are modulated by Sirt1 in mammals. HIF-2α is only present in vertebrates and regulates expression of prosurvival factors under hypoxia and other adverse environmental conditions (*2*). HIF-2 signaling, regulated in part by hypoxia-induced acetylation, and Sirt1 augmentation of HIF-2 signaling, conferred through Sirt1/HIF-2α complex formation as well as by Sirt1-mediated deacetylation of acetylated HIF-2α, likely have a specialized role in higher metazoans. Signaling from Sirt1 to HIF-2α could

be induced by other environmental stresses besides hypoxia that alter pyridine nucleotide homeostasis and activate HIF-2α signaling. Identifying the relevant environmental stressors that induce Sirt1/HIF-2α signaling and defining the role of Sirt1/HIF-2α signaling in the regulation of protective cellular mechanisms in mammals may provide novel therapeutic opportunities for human disease states.

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Did Warfare Among Ancestral Hunter-Gatherers Affect the Evolution of Human Social Behaviors?

Samuel Bowles[1,2]

Since Darwin, intergroup 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 intergroup violence sufficient to influence 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 intergroup conflicts would have had substantial effects, allowing the proliferation of group-beneficial behaviors that were quite costly to the individual altruist.

Intergroup 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*), p. 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 (*2–4*), however, lethal intergroup 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 archaeological traces other than skeletal remains.

In light of the available archaeological and ethnographic evidence, could war among ances-

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tral 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 quantify the relation 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 prehistoric 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 Late Pleistocene and early Holocene.

The absence of archaeological evidence of persistent economic and political differentiation between families before about 24,000 years ago (*15*) indicates that the most informative data for understanding Late Pleistocene 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, and equestrian hunting populations. Because 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 intergroup 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 were 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 sources included 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 Fig. 1. [Details and additional caveats concerning these and the data to follow appear in (*17*).]

Intergroup conflict and the evolution of social behaviors. Although both genetic and cultural transmission are probably 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 suffer adverse within-group selection. But it 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 intergroup contests. In game theoretic terms, defense or predation is a public good (participating is 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 in which 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

Table 1. Fraction of total mortality due to warfare (δ): summary statistics. 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.

	Weighted mean	Arithmetic mean	Median
Archaeological	0.12	0.14	0.12
Ethnographic	0.16	0.14	0.13–0.15
All	0.14	0.14	0.12

Fig. 1. Sources of archaeological (filled squares) and ethnographic (filled dots) evidence on warfare and genetic (open dots) data on between-group differences.

suffer high mortality due to inadequate parental care. The second is that, as with chimpanzees (*18*), weaker groups cede territory, thereby redistributing fitness-relevant resources between the groups.

I consider a large population made up of subpopulations that 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 intergroup 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 κ, a group is paired for a contest with another group and survives with probability λ, 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 in the next generation is thus 1, 2, or 0 with probabilities $(1 - \kappa)$, $\kappa\lambda$, and $\kappa(1 - \lambda)$, respectively, so the expected size is $w_j = 1 - \kappa + 2\kappa\lambda$. The effect of the prevalence of altruists on the expected size of the group in the next generation is the likelihood of a contest (κ), 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 (λ_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

Table 2. Archaeological and ethnographic evidence on the fraction (δ) of adult mortality due to warfare. "Before present" indicates before 2008.

Site	Approx. date (years before present)	Author (date)	δ
Archaeological evidence			
British Columbia (30 sites)	5500–334	Cybulski (1994)	0.23
Nubia (site 117)	14–12000	Wendoff (1968)	0.46
Nubia (near site 117)	14–12000	Wendoff (1968)	0.03
Vasiliv'ka III, Ukraine	11000	Telegin (1961)	0.21
Volos'ke, Ukraine	"Epipalaeolithic"	Danilenko (1955)	0.22
S. California (28 sites)	5500–628	Lambert (1997)	0.06
Central California	3500–500	Moratto (1984)	0.05
Sweden (Skateholm I)	6100	Price (1985)	0.07
Central California	2415–1773	Andrushko *et al.* (2005)	0.08
Sarai Nahar Rai, N.India	3140–2854	Sharma (1973)	0.30
Central California (2 sites)	2240–238	Jurmain (2001)	0.04
Gobero, Niger	16,000–8200	Sereno *et al.* (2008)	0.00
Calumnata, Algeria	8300–7300	Chamla *et al.* (1970)	0.04
Ile Teviec, France	6600	Newall *et al.* (1979)	0.12
Bogebakken, Denmark	6300–5800	Newall *et al.* (1979)	0.12
Ethnographic evidence			
Population, region	Dates	Author (date)	δ
Ache, Eastern Paraguay[*]	Precontact (1970)	Hill and Hurtado (1996)	0.30
Hiwi, Venezuela-Colombia[*]	Precontact (1960)	Hill *et al.* (2007)	0.17
Murngin, NE Australia[*†]	1910–1930	Warner (1931)	0.21
Ayoreo, Bolivia-Paraguay[‡]	1920–1979	Bugos (1985)	0.15
Tiwi, N. Australia[§]	1893–1903	Pilling (1968)	0.10
Modoc, N. California[§]	"Aboriginal times"	Ray (1963)	0.13
Casiguran Agta, Philippines[*]	1936–1950	Headland (1989)	0.05
Anbara, N. Australia[*†‖]	1940–1960	Hiatt (1965)	0.04

[*]Foragers.　[†]Maritime.　[‡]Seasonal forager-horticulturalists.　[§]Sedentary hunter-gatherers.　[‖]Recently settled.
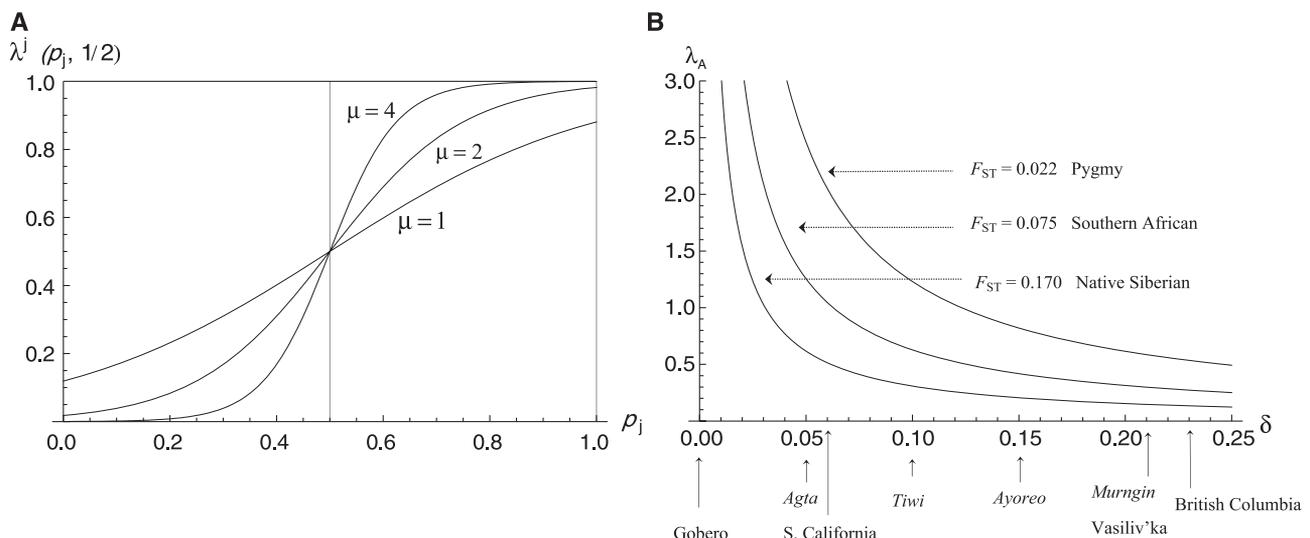
Fig. 2. (**A**) Contest success probabilities [$\lambda^j (p_j, p) = \lambda^j (p_j, \frac{1}{2})$] for group j if half of the opposing group are altruists. The parameter μ determines the slope of the function (λ_A) at $p_j = 0.5$. This success function differs from that of the Lanchester model (*45*) 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*). (**B**) Wartime mortality (δ) and the effect of altruism on success in conflicts (λ_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}). Shown are the values of c^* consistent with Eq. 6 for the estimated F values from (*12*) [see also (*17*)]. The representative values of δ are from Table 2. Populations on the horizontal axis in italics are from the ethnographic sample; the rest are from the archaeological sample.

of group j's membership that are altruists, p and p' be the altruist-fraction of the metapopulation in a given and subsequent generation, respectively, and $\Delta p \equiv p' - p$. Then, using the Price equation (20) and assuming a constant metapopulation size, the evolution of altruism (summarized by Δp) can be expressed as a between-group effect plus a within-group effect:

$$\Delta p = \text{var}(p_j)\beta_G + E\{\text{var}(p_{ij})\}\beta_i \quad (1)$$

The terms $\text{var}(p_j)$ and $E\{\text{var}(p_{ij})\}$ are, respectively, the between-group and within-group genetic variance. ($E\{\}$ indicates a size-weighted average over groups.) The coefficient β_G is the effect of variation in p_j on the average fitness of members of group j (w_j), which (see above) is

$$\beta_G \equiv dw_j/dp_j = \kappa 2\lambda_A \quad (2)$$

The coefficient β_i is the effect of variation in p_{ij} (namely, switching from a nonaltruist to an altruist) on the fitness of an individual in group j (w_{ij}):

$$\beta_i \equiv dw_{ij}/dp_{ij} = -c + \kappa 2\lambda_A/n \quad (3)$$

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 Eq. 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 nonrandom 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 Eq. 1 to give a condition for the proliferation of the altruistic trait (namely, $\Delta p > 0$):

$$F_{ST}/(1 - F_{ST}) > -\beta_i/\beta_G \quad (4)$$

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 multilevel selection analog to Hamilton's rule for the proliferation of altruism by kin selection.
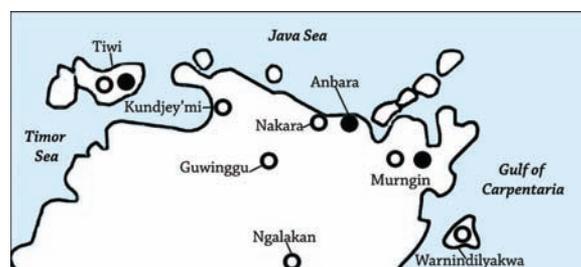
With these results, the condition for an altruistic allele to proliferate (Eq. 4) can be written as

$$F_{ST}/(1 - F_{ST}) > c/\kappa 2\lambda_A - 1/n \quad (5)$$

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

$$c^* = \kappa 2\lambda_A \{F_{ST}/(1 - F_{ST}) + 1/n\} \quad (6)$$

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 is 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 consisting of just a few of the 100 or so bones in an adult human (excluding the small bones of the hands and feet). The remains of 2185 prehistoric people from Californian sites are accessible to researchers in a museum collection that totals only 12,044 bones (excluding hands and feet); more than 90% of the individuals' bones are absent (22).

Moreover, although some osteological evidence is indicative of ongoing intergroup violence (simultaneous burials, severed limbs, and other evidence of trophy taking, for example), one cannot always distinguish between deaths due to intergroup 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 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% 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 2 gives the resulting estimates.

Ethnographic evidence. Most ethnographic studies of premodern 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 nonequestrian foragers, detailed accounts provide examples of intergroup conflict of exceptional brutality among Aboriginal Australians, Eskimos, and other groups (3, 26, 27), 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 absence may be the result of recent state interventions (28, 29). For eight populations, ethnographic studies allow estimates of the deaths due to warfare as a fraction of total mortality (summarized in Table 2). 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 me to treat 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 κ, the per-generation probability of such a decisive conflict.

Table 3. Largest cost (c^*) for an altruistic trait to proliferate given estimates of genetic differentiation and mortality in intergroup hostilities (δ) among three Arnhem Land, Australian hunter-gatherer populations. The entries are given by Eq. 6, where $\kappa = 2\delta$. Genetic differentiation ($F_{ST} = 0.040$) is among seven groups [including Tiwi and Murngin (see Fig. 3)] and is from (34) [see also (17)]; δ is from Table 2; $\lambda_A = 2$; $n = 26$, the size of a single generation in a coalition of three groups of the census size considered to be typical of nonequestrian, non-Arctic foragers during the Late Pleistocene (44).

	Murngin $\delta = 0.207$	Tiwi $\delta = 0.100$	Anbara $\delta = 0.045$
$n = 26$	0.133	0.064	0.029
$n = \infty$	0.069	0.033	0.015

Fig. 3. Data sources in Arnhem Land, Australia, for ethnographic evidence on warfare (filled dots) and genetic differentiation (open dots). [Source: Table 2 and (34)] The maximum distance between pairs of groups shown is about 600 km.

Java Sea
Tiwi
Timor Sea
Kundjey'mi
Anbara
Nakara
Guwinggu
Murngin
Gulf of Carpentaria
Ngalakan
Warnindilyakwa

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 δ, 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 (λ_A) and the extent of genetic differentiation among groups (F_{ST}). There is no way to estimate λ_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 Fig. 2A. For the contest success functions illustrated, the assumption that the success function is approximately linear (λ_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 10% 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 in 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 one for this study. Excluding those populations that currently live at such a distance 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-gatherer groups (17). The mean F_{ST} of the 18 estimates is 0.074, whereas 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, 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 $c^* = 0.03$, for example, is a quite substantial cost, one that in the absence of intergroup 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 nonaltruistic 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 δ 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 Late 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 10,000 years ago (33). The availability of archaeological, ethnographic, and genetic data for this region makes it a remarkable laboratory for this investigation (Fig. 3).

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 Murngin) in that relatively small area (34). The estimates of c^* for these populations (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 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 Eq. 6 and thus eliminating the direct benefit accruing to the altruist.

To explore the importance of variations in λ_A, Fig. 2B uses the extreme F_{ST} values for differentiation between ethno-linguistic groups (Native Siberian and Pygmy) and the median of these values (South African) to show the combinations values of λ_A and δ such that the between-group selection would offset a $c^* = 0.03$. Figure 2B indicates that for plausible values of the effect of altruistic behaviors on a group's chances of prevailing in contests (λ_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 exceeding 2% 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 intergroup 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 genetic 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 prehistory, lethal group conflict may have been frequent enough to 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 intergroup 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.

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REPORTS

Late Pleistocene Demography and the Appearance of Modern Human Behavior

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The origins of modern human behavior are marked by increased symbolic and technological complexity in the archaeological record. In western Eurasia this transition, the Upper Paleolithic, occurred about 45,000 years ago, but many of its features appear transiently in southern Africa about 45,000 years earlier. We show that demography is a major determinant in the maintenance of cultural complexity and that variation in regional subpopulation density and/or migratory activity results in spatial structuring of cultural skill accumulation. Genetic estimates of regional population size over time show that densities in early Upper Paleolithic Europe were similar to those in sub-Saharan Africa when modern behavior first appeared. Demographic factors can thus explain geographic variation in the timing of the first appearance of modern behavior without invoking increased cognitive capacity.

The Upper Paleolithic (UP) transition, which occurred in Europe and western Asia about 45 thousand years ago (ka) (*1*, *2*), and later in southern and eastern Asia (*3*, *4*), Australia (*5*, *6*), and Africa (*7*), is seen by many as marking the origins of modern human behavior. UP material culture, usually referred to as the Late Stone Age (LSA) in Africa, is characterized by a substantial increase in technological and cultural complexity, includ-ing the first consistent presence of symbolic behavior, such as abstract and realistic art and body decoration (e.g., threaded shell beads, teeth, ivory, ostrich egg shells, ochre, and tattoo kits); systematically produced microlithic stone tools (especially blades and burins); functional and ritual bone, antler, and ivory artifacts; grinding and pounding stone tools; improved hunting and trapping technology (e.g., spear throwers, bows, boomerangs, and nets); an increase in the long-distance transfer of raw materials; and musical instruments, in the form of bone pipes (*1*, *2*, *5*, *7–9*).

In Europe and western Asia, the UP transition happened relatively rapidly, with most of the characteristic features listed above appearing (the "full package"), and is thought to coincide with the appearance of anatomically modern humans (AMH) in a region previously occupied by Neandertals (*10*). In southern Siberia and northeast Asia, microlithic technology appears between 43 and 27 ka (*11*), but a fuller UP package is not evident until ~22 ka (*12*). The evidence from south and southeast Asia and Australia also points to a more gradual accumulation of modern behavioral traits (ornamentation, use of ochre, and possibly rock art) (*3–6*). These are thought to first appear soon after the initial expansions of AMH into the regions but only become wide-spread later on, ~30 ka (*4*) and ~20 ka, if not later (*5*), in south Asia and Australia, respectively. In Africa, the idea of a single transition has been

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