

Group Competition, Reproductive Leveling, and the Evolution of Human Altruism

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Humans behave altruistically in natural settings and experiments. A possible explanation—that groups with more altruists survive when groups compete—has long been judged untenable on empirical grounds for most species. But there have been no empirical tests of this explanation for humans. My empirical estimates show that genetic differences between early human groups are likely to have been great enough so that lethal intergroup competition could account for the evolution of altruism. Crucial to this process were distinctive human practices such as sharing food beyond the immediate family, monogamy, and other forms of reproductive leveling. These culturally transmitted practices presuppose advanced cognitive and linguistic capacities, possibly accounting for the distinctive forms of altruism found in our species.

Darwin thought that the “moral faculties” had proliferated among early humans because a tribe of “courageous, sympathetic and faithful members who were always ready to...aid and defend each other... would spread and be victorious over other tribes” (1, p. 134). Recent experiments have extensively documented altruistic behaviors not only in laboratories but also among hunter-gatherer populations (2–4). But in order for the survival of more altruistic groups in competition with other groups to account for the evolution of a predisposition to act altruistically, the group extinction process would have to be strong enough to offset the lower fitness of altruists compared to other members of their group. For this to be the case, there would have to be substantial differences in the fraction of altruists in groups, which is thought to be unlikely because migration among groups tends to limit between-group differences in group composition. Thus, many have concluded that between-group genetic differences are too small for selective group extinction to offset the within-group selective pressures that oppose the evolution of a genetic predisposition to behave altruistically [(5), but see also (6)].

However, early humans lived under conditions such that selective group extinction might have been a powerful evolutionary force. Culturally transmitted norms supporting resource and information sharing, consensus decision-making, collective restraints on would-be aggrandizers, monogamy, and other reproductive leveling practices that reduced within-group differences in fitness may have attenuated the selective pressures to which altruists are subject (7–11). The impact of intergroup competition is heightened by the fact that although group aggression is not uniquely human (12), among humans it is extraordinarily lethal (13).

Models (14), computer simulations (15), and empirical studies (16) have confirmed that intergroup competition could influence the evolution of culturally transmitted behavior. This study investigates whether, as an empirical matter, intergroup competition and reproductive leveling might have allowed the proliferation of a genetically transmitted predisposition to behave altruistically. To determine the facts necessary for this inquiry, a model was developed that captures the main aspects of ancestral human genetic differentiation, between-group competition, and group social structure.

Framework for the empirical analysis. Consider a large metapopulation of individuals living in partially isolated subpopulations (called demes). Altruists (A's) take an action costing c that confers a benefit b on an individual randomly selected from the n members of the deme. (Payoffs are given in Table 1, and the model and notation are summarized in Table 2.) A's are bearers of a hypothetical “altruistic allele”; those without the allele (N's) do not behave altruistically. Reproduction is asexual. In the absence of reproductive leveling, individual fitness is identical to the payoffs in Table 1. For example, an A who interacts solely with A's will expect a number of offspring surviving to reproductive age that is $b - c$ greater than the fitness of an N who interacts only with N's.

Let $p_{ij} = 1$ if individual i in deme j is an A with $p_{ij} = 0$ otherwise. Let p_j be the fraction of deme j 's membership that are A's; p and p' be the A-fraction of the metapopulation in a given and subsequent generation, respectively; and $\Delta p \equiv p' - p$. Then, following Price (17) and assuming the metapopulation size does not change, we can express the possible evolution of altruism as summarized by Δp as a between-deme effect plus a within-deme 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-deme and within-deme genetic

variance. ($E\{\}$ indicates a weighted average over demes.) The coefficient β_G is the effect of variation in p_j on the average fitness of members of deme j (w_j); β_i is the effect of variation in p_{ij} (namely, switching from an N to an A) on the fitness of an individual in deme j (w_{ij}). A behavior is altruistic if adopting it lowers one's expected fitness while increasing the average fitness of one's deme (18). Given this definition, we are interested in the case where β_i is negative and β_G is positive.

Using Eq. 1, we see that whether altruism evolves ($\Delta p > 0$) depends on the outcome of a race in which the between-selection process promoting its spread [$\text{var}(p_j)\beta_G$] competes with the within-selection process tending to eliminate it ($E\{\text{var}(p_{ij})\}\beta_i$). For the between-deme effect to exceed the within-deme effect (rearranging Eq. 1), it must be that

$$\frac{\text{var}(p_j)}{E\{\text{var}(p_{ij})\}} > -\beta_i/\beta_G \quad (2)$$

The left-hand side of this condition is a measure of positive assortment arising from the fact that if the fraction of A's in demes differ [that is, $\text{var}(p_j)$ is positive], then A's are more likely than N's to interact with A's.

Because the within-deme benefits of altruism are randomly distributed, between-deme differences in the prevalence of A's [i.e., $\text{var}(p_j) > 0$] is the only reason why A's are more likely than N's to interact with A's and thus to benefit mutually. But if A's are likely to benefit for this reason, they are also more likely to compete over deme-specific resources (19, 20). I assume the most stringent form of local density-dependent constraints on reproductive output: Sites are saturated so that territorial expansion is required for deme growth. Thus, altruism can proliferate only by helping a deme to acquire more territory, not by any of the other ways that members of predominantly altruistic demes might produce more surviving offspring.

Selective group extinction. Selective extinction may allow the evolution of altruism if predominantly altruistic demes are more likely than other demes to survive between-deme contests and to colonize and repopulate the sites vacated by demes that fail (21). This process is captured by the term β_G , the size of which is determined by the frequency of contests, the fitness effects of surviving a contest, and the contribution of altruists to surviving.

In every generation with probability κ , each deme engages in a “contest.” (A contest may be a

Table 1. Payoffs to within-deme interactions. Entries are the payoffs of the row individual when interacting with an individual whose type is given by the column head.

	Altruist	Not
Altruist (A)	$1 + b - c$	$1 - c$
Not (N)	$1 + b$	1

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hostile encounter or an environmental challenge without direct deme interaction.) Demes that fail are eliminated, and surviving demes repopulate the vacated sites. Early human demes probably faced frequent intergroup, environmental, and other challenges resulting in occasional fatalities or territorial losses or gains [more closely resembling boundary skirmishes among chimpanzees (22) than this all-or-nothing deme-extinction scenario]. I show (13) that estimates of long-term fitness effects of continuous low-level losses or gains are equivalent to a complete extinction-repopulation scenario occurring infrequently.

Demers are the same size (normalized to 1), except that demes that have occupied the site of an eliminated deme are momentarily of size 2 (and eliminated demes are of size zero). The surviving deme divides, forming two daughter demes of equal size. Let the probability that the deme survives be λ . The size of deme 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 A's on the expected size of the deme in the next generation (that is, $\beta_G \equiv dw_j/dp_j$) is the likelihood of a contest (κ), times the effect on deme size of surviving or not (2), times the effect of the prevalence of A's on the probability of a deme surviving should a contest occur (that is, $d\lambda/dp_j \equiv \lambda_A$); so $\beta_G = \kappa 2\lambda_A$. There is no way to estimate λ_A empirically, so I explore two alternative values (13): $\lambda_A = 1$ is derived from a model in which all-A and all-N demes (respectively) survive and fail with certainty should a contest occur; whereas if $\lambda_A = 1/2$, an all-A deme survives with probability $3/4$ and an all-N deme survives with probability $1/4$.

Reproductive leveling. Distinctive human practices within groups also created a favorable niche for the evolution of altruism. Individual differences in size, health, behavior, and other influences on access to scarce resources are typically reflected in differences in reproductive success. Among some primates (23, 24), and especially among humans, reproductive leveling attenuates this relation. Because altruists receive lower payoffs than other deme members (by the definition of altruism), they benefit from reproductive leveling, resulting in a reduction of the term β_i .

To see how this works, suppose an N were instead an A. In the absence of reproductive leveling, its fitness would be less by an amount c . But the individual would also have a $1/n$ chance of garnering the benefit b , which is distributed randomly to members of the group. Additionally, by increasing the chance of survival of the deme (in which case, like every member of the surviving deme, it will be doubled), it also contributes directly to its own fitness an amount equal to $1/n$ (i.e., the effect of the switch from N to A on p_j) times β_G (the effect of variations in p_j on the average fitness of the deme). Thus

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

Reproductive leveling can now be introduced by representing it as a convention, conformity to which is in the interest of each deme member (25). Let some portion of the payoffs initially acquired by an individual be distributed equally among all deme members. Reproductive leveling then takes the form of a proportional deduction at rate τ of each member's payoffs, the proceeds of which are distributed equally to all members of the deme. The effect is to reduce within-deme fitness differences between A's and N's from $-c$ to $-(1 - \tau)c$, so $\beta_i = -(1 - \tau)c + b/n + \kappa 2\lambda_A/n$.

Positive assortment and the evolution of altruism. Substituting these values for β_i and β_G in Eq. 1, we have

$$\Delta p = \text{var}(p_j)\kappa 2\lambda_A - E\{\text{var}(p_{ij})\}\{(1 - \tau)c - (b + \kappa 2\lambda_A)/n\} \quad (4)$$

We will assess this condition with genetic data from recent hunter-gatherer populations, using a commonly measured statistic from population genetics, the fraction of the total genetic variance at a locus that is between groups, also known as Wright's inbreeding coefficient (26): $F_{ST} \equiv \text{var}(p_j)/[\text{var}(p_j) + E\{\text{var}(p_{ij})\}]$. Using this definition, we rewrite Eqs. 2 and 4 and find that the A's share of the metapopulation will increase if

$$\frac{F_{ST}}{(1 - F_{ST})} > -\frac{\beta_i}{\beta_G} = \frac{(1 - \tau)c - b/n}{\kappa 2\lambda_A} - \frac{1}{n} \quad (5)$$

If n is large, this is approximated by

$$\frac{F_{ST}}{(1 - F_{ST})} > \frac{(1 - \tau)c}{\kappa 2\lambda_A} \quad (6)$$

Like Hamilton's rule for the evolution of altruism by inclusive fitness, this model thus yields a condition indicating the minimum degree of positive assortment necessary to allow altruism to proliferate. The left-hand term, like Hamilton's degree of relatedness (r), is a measure of positive assortment; but here assortment arises solely from between-deme differences in the prevalence of A's. The right-hand term in Eq. 6 is the ratio of individual costs to group-level benefits. We now ask if ancestral humans are likely to have lived under conditions such that Eqs. 5 or 6 would be satisfied. Table 3 is a summary of the main parameters and the estimated range of empirically plausible values.

Empirical estimates of F_{ST} . Wright [(27), p. 203] speculated that an equilibrium F_{ST} among human groups—namely, that which would balance the offsetting effects of migration and drift—might be about 0.02, a value that would preclude interdemal competition as an important evolutionary force. But most empirical estimates are considerably larger. The measures of genetic differentiation in Table 4 are from recent foraging populations whose population structure, geographical and linguistic proximity, and livelihood may resemble those of foraging bands of the late Pleistocene and early Holocene (about 150,000 to 10,000 years before the present). These estimates are based on genetic material, most of which was collected before the mid-1970s, and in most cases are averages over a large number of genetic systems and over F -statistics among a large number of subpopulations. A nested three-level hierarchy of measures of genetic differentiation is estimated, depending on the size of the subpopulation units (13): F_{DG} measures genetic differentiation among demes (D) in the same ethno-linguistic group (G), whereas F_{GT} and F_{DT} , respectively, measure differentiation among groups and demes in a metapopulation (T). If most competition is between demes across ethno-linguistic boundaries, then F_{DT} is the relevant statistic.

I think it is unlikely that Table 4 overestimates the relevant degree of genetic differentiation among early humans. First, extreme

Table 2. Summary of model and notation. b and c : benefits and costs to deme members; p_k : percent of deme k that are A's; and p : percent of metapopulation that are A's.

Notation	Eq. no.	Equation	Comment
Generic Price equation (PE)	1	$\Delta p = \text{var}(p_j)\beta_G + E\{\text{var}(p_{ij})\}\beta_i$	Δp = between deme + within deme
Generic PE condition for A to increase	2	$\text{var}(p_j)/E\{\text{var}(p_{ij})\} \equiv F_{ST}/(1 - F_{ST}) > -\beta_i/\beta_G$	F_{ST} = between-deme var/total var
Effect of A on deme-average fitness (β_G)		$\beta_G \equiv dw_j/dp_j = \kappa(dw_j/d\lambda)(d\lambda/dp_j) = \kappa 2\lambda_A$	κ = probability of interdemal contest
Effect of A on individual fitness (β_i)		$\beta_i \equiv dw_{ij}/dp_{ij} = -(1 - \tau)c + b/n + \kappa 2\lambda_A/n$	τ = extent of reproductive leveling
Condition for A's to increase (Price equation)	4	$\Delta p = \text{var}(p_j)\kappa 2\lambda_A - E\{\text{var}(p_{ij})\}\{(1 - \tau)c - (b + \kappa 2\lambda_A)/n\}$	Δp = between-deme + within-deme effect
Condition for A's to increase	5	$F_{ST}/(1 - F_{ST}) > -\beta_i/\beta_G = \{(1 - \tau)c - b/n\}/\kappa 2\lambda_A - 1/n$	Larger F_{ST} favors A's.
Condition for A's to increase (if $n = \infty$)	6	$F_{ST}/(1 - F_{ST}) > (1 - \tau)c/\kappa 2\lambda_A$	> individual cost/deme benefit

climate variability during the late Pleistocene (fig. S3) probably induced frequent deme extinctions, population crashes, and subsequent growth, resulting in the colonization of new sites by small propagules. Natural experiments [e.g., with the plant *Silene dioica* (28)] suggest that the effect may be a considerable elevation of between-group genetic variance. Second, genetic differentiation among a subspecies of chimpanzees (*Pan troglodytes schweinfurthii*) whose spatial distribution and demographic history may resemble those of early humans (29) is substantially higher than the median of the estimates in Table 4 ($F_{ST} = 0.102$).

However, genetic differentiation at the locus of an allele that is expressed in an altruistic behavior may differ from that estimated for neutral loci (those not under selection) such as those in Table 4. First, an altruistic allele would be (by definition) under directional selection. This would be expected to reduce interdemic genetic differentiation at least in the very long run, because in the absence of offsetting effects, the frequency of the A's in the population will eventually go to zero. However, this tendency may not work over time scales relevant to human demes. Simulations (13) show that even for very strong selection against the A's and for plausible initial distributions of A's in demes, the F_{ST} rises for tens of generations. For moderate selection against the A's, the F_{ST} may rise for more than a hundred generations before falling. Because fission and extinction events that enhance interdemic variance are likely to be an order of magnitude more frequent than this, it appears that high levels of F_{ST} could persist indefinitely. Even with random fission (and relatively small demes), additional simulations (25) show that exceptionally strong directional selection against the A's ($c = 0.1$) is compatible with the indefinite maintenance of high levels of F_{ST} .

Second, altruists will sometimes be able exclude nonaltruists from their demes, resulting in what Eshel and Cavalli-Sforza called "selective assortment" (30, 31). This is particularly common when demes fission, a process Hamilton (32) called "associative tribe splitting." Directed migration (33) will also enhance between-deme variance and reduce within-deme variance. Here, selective assortment is contingent on past behavior that is itself an observable expression of the altruistic allele. As a result, the only way

an N can mimic the A's so as to evade their choosiness is to adopt the altruistic behavior itself and thus to bear its costs. Thus, the instability arising in the case of assortment by "green beards" (34) does not arise.

But there is nonetheless an impediment to selective assortment that is sometimes overlooked: Exclusion of N's is likely to be costly for the A's, whereas the associated benefits are shared by all deme members. However, it is not implausible that altruists would undertake some moderate level of N-exclusion as a contribution to the public good. There is ample ethnographic evidence (11) that foragers practice selective assortment when they ostracize or shun individuals who violate behavioral norms. Models and simulations (35) confirm that these practices can proliferate when rare and persist indefinitely in a plausible evolutionary dynamic. Moreover, it is readily shown (13) that a modest amount of selective assortment generates substantial levels of between-deme differences.

Within-deme selection. Although the effects of most forms of reproductive leveling cannot be estimated, the degree of within-deme resource sharing is known from empirical studies of the acquisition and consumption of nutrition among foragers (13). On this basis, I take $\tau = 2/3$ as a plausible benchmark with $1/3$ an alternative value (13).

The appropriate value of n is the number of deme members of a breeding generation (about a third of the census size). The median band (cen-

sus) size in the most comprehensive survey (13) is 19. Individual bands may have competed for survival, but it is likely that bands in coalition also engaged in contests. A plausible benchmark is that a deme is five bands, giving $n = 32$; I will also consider very large (strictly, infinite) demes.

Plausible values of c and b will depend on the particular altruistic behavior in question. For example, a warning call would have a different b and c than defending the community against hostile neighbors. To facilitate the exploration of a variety of altruistic behaviors, I present results for a given $b = 0.05$ and c varying from 0 to 0.08. (Eqs. 5 and 6 make it clear that for sizable demes, b is of little importance.)

Deme extinction. The extent of hostile group interactions during the late Pleistocene and early Holocene may be suggested by climatic data, hunter-gatherer demographics, archaeological evidence, and recent histories of foraging peoples, and is a matter of some debate [the evidence is reviewed in (13)].

We know from ice and deep-sea cores that average temperature during the late Pleistocene varied by as much as 8°C over periods of less than two centuries—the difference in average contemporary annual temperatures between Cape Town and Mombasa, 4000 km to the north (fig. S3). Mortal challenges resulting from climatic adversity must have been frequent, as well as from hostile interactions among groups migrating over unfamiliar terrain without established arrangements

Table 4. Genetic differentiation among 13 hunter-gatherer subpopulations (13). The median and mean values (respectively) are 0.076 and 0.081. The median and mean for the F_{DT} estimates are 0.081 and 0.093.

Population	Index	F
Indigenous circumpolar Eurasian populations	F_{DT}	0.076
Native Siberian populations	F_{DT}	0.170
Native Siberian populations	F_{DG}	0.114
!Kung demes (Southern Africa)	F_{DG}	0.007
Southern African groups	F_{GT}	0.075
Southern African demes (from 18 groups)	F_{DT}	0.081
Aboriginal Australians	F_{GT}	0.042
Kaiadilt-Lardiil groups (Australia)	F_{DT}	0.081
Asmat-Mappi (Lowland Western New Guinea)	F_{DT}	0.056
Mbuti (Central Africa)—San (Southern Africa)	F_{GT}	0.149
Aka (Central Africa between "villages" in the same group)	F_{DG}	0.042
Aka (between groups)	F_{GT}	0.057
Aka (between "villages" in all groups)	F_{DT}	0.097

Table 3. Parameter estimates. Benchmark values are in bold. Entries not in bold are alternative values ($\delta = 0.4$ not used).

Determinant		Range explored	Comment/method of estimation (13)
Interdemic genetic differentiation	F_{ST}	0.007–0.170; 0.076	Genetic markers (recent foragers)
Reproductive leveling	τ	0.66 , 0.33	Food sharing (recent foragers)
Gains – losses from contests per generation	δ	0.30 , (0.40)	Archaeological and ethnographic evidence
Per-generation probability of a decisive (2,0) contest	κ	= $\delta/2$	Based on estimates of mortality in ongoing conflict
Effect of percent altruists on deme survival	λ_A	$1/2$, 1	Arbitrary (see Fig. 1)
Effective deme size (one-third of census size)	n	32 , ∞	Coalition of 5 median-sized bands
Cost to altruist	c	0.0 to 0.08	Depends on behavior under consideration
Benefits to deme members (without a contest)	b	0.05	As immediately above

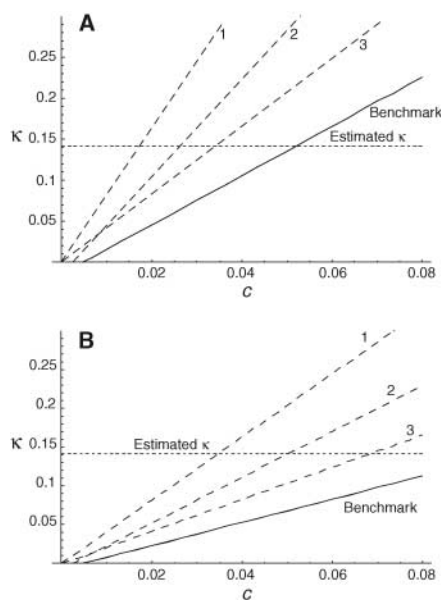


Fig. 1. Conditions for the evolution of altruism by selective extinction and reproductive leveling if $F = 0.076$. The solid lines are the benchmark values estimated in the text ($n = 32$, $\tau = 0.66$). Line 1: $n = \infty$, $\tau = 0.33$; line 2: $n = 32$, $\tau = 0.33$; line 3: $n = \infty$, $\tau = 0.66$. Points above each line give combinations of c and κ such that altruism would proliferate according to Eqs. 5 and 6. (A) $\lambda_A = 1/2$; and (B) $\lambda_A = 1$. For both panels, $b = 0.05$.

for peaceful coexistence. Frequent catastrophic mortality is the most plausible way to reconcile two facts about hunter-gatherer demography—namely, that human population grew extraordinarily slowly or not at all for the 100,000 years prior to 20,000 years before the present (36), yet models and data on hunter-gatherer demographics show that they are capable of growth rates exceeding 2% per annum (37).

A few archaeological sites from the late Pleistocene suggest that exceptionally lethal warfare took place and that violence intensified during periods of climatic adversity and resource stress (13). Deaths due to warfare constitute a substantial fraction of all deaths among foragers, averaging 13% on the basis of archaeological data (violent deaths, table S3) and 15% on the basis of ethnographic studies. This is much more than for Europe and the United States in the 20th century (less than 1% of male deaths). Territorial loss or gains due to warfare among a small sample of foraging groups averaged 16% per generation. Based on averages of three large samples from the ethnographic record (table S4), war was “rare” in only a fifth of the hunter-gatherer societies and “continuous” in a third.

I show (13) that the level of ongoing hostility indicated by these data would produce fitness effects equivalent to the extinction-repopulation scenario modeled above occurring every five to seven generations, the latter figure ignoring war casualties and considering only the demographic effects of territorial losses and gains. Neither

estimate includes extinctions induced directly by climate change or other events unrelated to war. I use the smaller estimate of the frequency of conflicts ($\kappa = 1/7$).

Discussion. The above estimates are subject to substantial error given that they are inferences about conditions occurring tens of thousands of years ago for which very little direct evidence is available. With this caveat in mind, suppose early humans' demographics and social practices resulted in genetic differentiation at the locus of an altruistic allele that was the magnitude of the median in Table 4 ($F = 0.076$). For the benchmark values of τ , n , and λ_A , the solid lines in Fig. 1 give the combinations of c and κ such that Eq. 5 is satisfied as an equality. More frequent contests or less costly forms of altruism (points above the line) allow altruism to proliferate. Dashed lines do the same for more stringent alternative parameter values. For example, for the estimated κ , if $c = 0.05$, altruism proliferates (for both values of λ_A) under the benchmark assumptions, but not for very large demes with limited reproductive leveling. Similar analysis for all of the data in Table 4 is presented in (13).

For many of the populations in Table 4 and for plausible parameter values, then, genetic differentiation is such that even very infrequent contests would have been sufficient to spread quite costly forms of altruism. Because the initial spread of altruism among humans could have been propelled by just a few of the vast number of late Pleistocene demes, the above data and reasoning suggest that selective deme extinction may be part of the account of the evolution of altruism. This is likely in the presence of appreciable levels of reproductive leveling (and not in its absence), suggesting an important role for culturally transmitted practices in creating a niche in which a genetic predisposition to behave altruistically might have evolved, and perhaps accounting for the distinctive aspects of human altruism not found in other species. Whether related processes of interdemographic competition might support the evolution of cooperative behaviors in the absence of highly developed cultural transmission and cognitive capacities [as has recently been suggested for eusocial insects (38)] is an empirical question that remains to be addressed.

Nothing here implies that a genetic disposition favoring human altruism exists, or that cultural or other possible explanations of human altruism are of lesser importance. The evidence does suggest that if such a disposition exists, it may be the result of a gene-culture coevolutionary process in which, as Darwin wrote, group conflict played a key role.

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Supporting Online Material

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References and Notes

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