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

Samuel Bowles

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:

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

The terms $\mathrm{var}(p_j)$ and $\mathrm{E}\{\mathrm{var}(p_{ij})\}$, 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 [$\mathrm{var}(p_j)\beta_G$] competes with the within-selection process tending to eliminate it ($\mathrm{E}\{\mathrm{var}(p_{ij})\}\beta_i$). For the between-deme effect to exceed the within-deme effect (rearranging Eq. 1), it must be that

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

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, $\mathrm{var}(p_j)$ 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., $\mathrm{var}(p_j) > 0$] 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.

Demes 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 $\lambda_A = ½$, an all-A deme survives with probability ¾ and an all-N deme survives with probability ¼.

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

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

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

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

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*): $F_{ST} \equiv \mathrm{var}(p_j)/[\mathrm{var}(p_j) + \mathrm{E}\{\mathrm{var}(p_{ij})\}]$. Using this definition, we rewrite Eqs. 2 and 4 and find that the A's share of the metapopulation will increase if

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

If n is large, this is approximated by

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

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 interdemic 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	$\Delta p = \mathrm{var}(p_j)\beta_G + \mathrm{E}\{\mathrm{var}(p_{ij})\}\beta_i$	Δp = between deme + within deme
Generic PE condition for A to increase	2	$\mathrm{var}(p_j)/\mathrm{E}\{\mathrm{var}(p_{ij})\} \equiv F_{ST}/(1-F_{ST}) > -\beta_i/\beta_G$	$F_{ST} \equiv$ 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 interdemic 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	$\Delta p = \mathrm{var}(p_j)\kappa 2\lambda_A - \mathrm{E}\{\mathrm{var}(p_{ij})\}\{(1-\tau)c - (b + \kappa 2\lambda_A)/n\}$	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 assortation 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 $\tau = ⅔$ as a plausible benchmark with ⅓ 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 (census) 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	**= δ/2**	Based on estimates of mortality in ongoing conflict
Effect of percent altruists on deme survival	λ_A	**½, 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

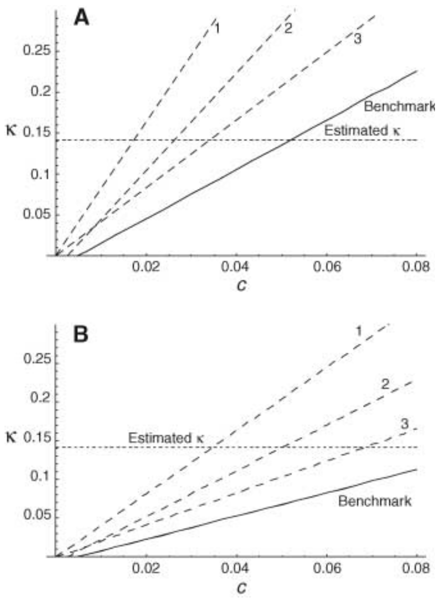

Fig. 1. Conditions for the evolution of altruism by selective extinction and reproductive leveling if $F = 0.076$. The solid lines are the benchmark values estimated in the text ($n = 32$, $\tau = 0.66$). Line 1: $n = \infty$, $\tau = 0.33$; line 2: $n = 32$, $\tau = 0.33$; line 3: $n = \infty$, $\tau = 0.66$. Points above each line give combinations of c and κ such that altruism would proliferate according to Eqs. 5 and 6. (**A**) $\lambda_A = ½$; 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 interdemic 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 euosocial 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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Supporting online materials for

Group competition, reproductive leveling and the evolution of human altruism

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Contents:

1. Background

The main features of this model – reproductive leveling and deme extinction – have received considerable attention among biologists interested in social behavior. Haldane (*1*):210-214 suggested that in a population of small endogamous "tribes," an altruistic trait might evolve because the "tribe splitting" that occurs when successful demes reach a certain size would by chance create a few successor demes with a very high frequency of altruists. This would enhance the force of selective extinction by increasing between-deme genetic differences. Wright (*2*):114 similarly held that 'isolation by distance' would support "statistical differences among local populations...[that] provide a possible basis for intergroup selection of genetic systems, a process that provides a more effective mechanism for adaptive advance of the species as a whole than does the mass selection that is all that can occur under panmixia." Like Wright and Haldane, Hamilton (*8*) remained skeptical that inter-demic competition would be a powerful evolutionary force; but he noted that if the assignment of members to successor demes following tribe-splitting was "associative" (p.137) rather than random, its importance would be enhanced.

From classic early works to recent contributions, phenotype-based models abstracting from the details of diploid genetic transmission have played a central role in the literature on inter-demic selection (*3-5*). Closest to the model here is the selective extinction model of Aoki (*6*). Though based on an entirely different derivation (with an explicit analysis of the dynamics of the between- and within-deme variances), the condition for altruism to evolve is the same in the two models. His equation (6) is

(S1) $f > s/(s+k)$

where $f = F_{ST}$, s = the selection coefficient measuring the cost of the altruistic behavior (that is, c in the notation of this paper) and k is a measure of "intensity of group selection" which (because the average probability of survival is ½) is equal $\kappa 2\lambda_A$. Using this equivalence and rearranging the equation S1 we have

(S2) $F_{ST}/(1-F_{ST}) > s/k = c/\kappa 2\lambda_A$

which is my equation (6) in the absence of reproductive leveling.

By contrast to the *selective extinction* model used here, the *selective emigration model* (*7*) works because the average fitness of members of predominantly altruistic demes is above the meta-population average and thus they contribute disproportionately to the next generation. (This is possible because sites are assumed not to be saturated and demes can either accommodate or export increments to their population.) For simplicity of comparison with the selective extinction model assume that n is sufficiently large so that we can ignore terms in $1/n$ and that $\tau = 0$.. Then $\beta_i = - c$ while the expected average fitness of members of deme j is $w_j = 1 + p_j(b - c)$ so $\beta_G \equiv dw_j/dp_j = b - c$. Using these values and equation (1) the condition for the A trait to increase (analogous to equations 2 and 6) is

(S3) $\text{var}(p_j)/\text{E}\{\text{var}(p_{ij})\} > - \beta_i/\beta_G = c/(b - c)$

or, upon rearranging,

(S4) $\text{var}(p_j)/\{\text{E}\{\text{var}(p_{ij})\} + \text{var}(p_j)\} \equiv F_{ST} > c/b$

which reproduces Hamilton's rule for the evolution of altruism by inclusive fitness with $r = F_{ST}$. Inspection of the estimates in table 4 shows that for this process to proliferate altruism, the benefits of altruism relative to the costs would need to be over ten for most groups.

2. Associative tribe-splitting.

An examination of fission among Amazonian tribal peoples ((*8*):198) reports that "fissioning ... keeps close kin together but separates them from more distant kin ... [T]he potential line of cleavage is furnished by the division in patrilineages." Among two pairs of Yanomamo daughter villages formed by a fission resulting from hostile relations within the parent deme "the net effect of lineal fission is to reduce the effective size of the village at the time of fission by a factor of four, relative to expectation from random fission." (*9*):179 (A reduction in effective size of this magnitude increases the level of equilibrium genetic differentiation by a factor of almost 4.) The authors conclude: "The process of village fission is strongly nonrandom socially, and results in pronounced genetic cohesion within, and great genetic differences between daughter villages." 194. About two-thirds of the genetic differentiation among South American tribes has been estimated to be the effect of associative fission (*10*) rather than isolation and drift stressed in the equilibrium F_{ST} formulations due to Wright (*11*). In these cases, genetic differentiation of demes is an unintended byproduct of lineal fission, as the alleles in question are not expressed in observable ways. For these alleles the between-deme genetic differentiation created by associative tribe splitting is already captured by the data in Table 4. But in the case of a behavioral trait such as altruism, one would expect deliberate associative fission and other forms of selective assortment, as altruists seek to exclude non-altruists from their demes.

Because excluding an N may be costly to an A, and because the benefits of the exclusion are shared with all members of the deme, selective assortment will frequently be a form of public goods provision (that is, an n-person prisoners' dilemma). Gintis and I modeled the evolution of a form of individually costly selective assortment behavior (*12*), in which substantial numbers of individuals who behave altruistically and ostracize those who violate a norm of altruistic behavior are sustained indefinitely, even when competing with cheaters who conform to the norm so as to avoid ostracism but do not contribute to the public good by ostracizing norm violators. The ethnographic literature suggests that selective assortment is common among some groups of foragers (see the works cited in (*13*) as well as (*14*))

To assess the effects on between-deme genetic differentiation of non-random deme fission we compare the expected between-deme variance resulting from associative fission and infinite deme size with that resulting from random fission and small deme size. Suppose an infinitely large "parent" deme splits into two "daughter" demes. We assume the secession is organized by a single head who seeks to compose a deme made up of individuals like himself, thereby setting aside the public goods aspect of selective assortment mentioned above and in the text. Because information about the past behavior of the members (the only basis of his selection of deme members) is noisy, with probability $(1-r)$ he selects randomly from the parent deme and with probability r he selects one of his own type. Thus r is the assortment coefficient for associative fission. If the departing head is an A, and p is the fraction of A's in the parent deme, the daughter deme will be composed of a fraction of A's approximately equal to $r + (1-r)p$. The fraction of A's among those remaining after the departure of the first daughter deme will be $2p - r-(1-r)p$. If the departing head is an N, the fraction of A's in his deme will be $p - rp$, and the fraction of those remaining who are A's is $2p - p + rp$. This process is summarized in Table S1

[Table S1 here]

If the departing head is drawn at random, he will be an A with probability p and the variance between the daughter deme (1) and the remaining deme (2), denoted $\mathrm{var}(p_j; r, \infty)$, (meaning the variance of the deme means p_j ($j \in [1,2]$) given r and assuming infinite deme size) is

$$\text{(S5)} \qquad \begin{aligned} \mathrm{var}(p_j; r, \infty) &= p[\{r+(1-r)p - p\}^2 + \{2p - r -(1-r)p -p\}^2]/2 \\ &\quad + (1 -p)[(p - rp - p)^2 + (2p - p + rp -p)^2]/2 \\ &= p(r-rp)^2 + (1-p)(-rp)^2 = p(1-p)r^2 \end{aligned}$$

This variance may be compared to the expected variance of deme means that occurs by chance (that is, in a manner equivalent to sampling error) with finite daughter deme size, n, or

$$\text{(S6)} \qquad \mathrm{var}(p_j; 0, n) = p(1-p)/n.$$

Now define the variance-effective daughter deme size, $n^*(r)$, as the size that in the absence of associative fission would produce the same level of between-deme variance as would associative fission of degree r in an infinite population. To find n^* we thus set $var(p_j; 0, n) = var(p_j; r, \infty)$ and solve for n, giving:

$$\text{(S7)} \qquad n^*(r) = 1/r^2$$

The implication of (S7) is this: Suppose that a propagule founder wished to include only his own type, but in just ten percent of the cases knew others' type and in the remaining cases guessed, choosing randomly. Then even if the parent deme is very large (strictly, infinite) the two daughter demes will be expected to differ in the frequency of A's by as much as if (in the absence of associative tribe-splitting) the size of the daughter demes were only 100.

3. Inter-demic genetic differentiation

I first define the various F-values used. I then turn to the sources, methods, and socio-demographic information concerning the estimates given in Table 4 as summarized in Table S2.

Demes are collections of people who are semi-isolated with respect to reproduction. Groups are collections of demes of the same ethno-linguistic, geographical or other unit.

Measures of genetic differentiation among a hierarchy of demographic units are due to Wright (*2, 15*). I define F_{LH} as the ratio of the genetic variance between units at a lower level (L) to the total genetic variance in a unit at a higher level (H). Three levels are used in Table 4 in ascending order of size: demes (D), groups (G) and the meta population (T). These relationships are summarized in Figure S1 and defined below.

[Figure S1 here]

The formulation below is for a locus with two alleles (that is not indexed to avoid notational clutter). Demes are indexed by j = 1...n and groups by k=1...m. The fraction of individuals bearing the A allele in demes and groups respectively is p_j and p_k, while p_{jk} is the fraction of deme j in group k that are A's, and n_k is the number of demes in group k. The fraction of A's in the meta-population is p (so the total variance is $p(1-p)$), and $\sum_y$ means summation over $y \in \{j,k\}$. Thus we have:

(S8) $F_{DT} = \{\sum_j (p_j - p)^2/n\}/p(1-p)$ differentiation among demes in the meta population;

(S9) $F_{GT} = \{\sum_k (p_k - p)^2/m\}/p(1-p))$ differentiation among groups in the meta population;

and for a given group,

(S10) $F_{DG}{}^k = \{\sum_j (p_{jk} - p_k)^2/n_k\}/p_k(1-p_k)$ differentiation among demes in a group.

It follows from these definitions that

(S11) $F_{DT} = F_{DG} + F_{GT} - F_{GT}F_{DG}$,

where F_{DG} is the average of $F_{DG}{}^k$ over groups.

Which of these measures of genetic differentiation is germane for our analysis depends on the level at which competition for survival took place. The importance of the appropriate definition of the units is suggested by estimates from the Yanomamo (an Amazonian tribal people), where three levels of grouping were studied: the F-value estimated for villages within the same mini-cluster in the same dialect group is 0.027, while that between villages in an entire dialect group is 0.084 and between villages in the meta-population is 0.137 (*9*). Similarly, as is evident from Table 4, differentiation between Aka villages in the same group is substantially less (0.042) than between villages drawn randomly from the entire population (0.097). Genetic differentiation among the !Kung is an order of magnitude less than among southern African populations generally.

[Table S2 here]

The sources, methods of calculation, and social and demographic characteristics of the groups studied are summarized in figure S2. A paper available from the author provides extensive additional information and compares these estimates to those what would be expected on the basis of Wright's expression for the equilibrium genetic differentiation among groups.

4. Deme extinction and survival.

I first consider the deme survival function and then estimate the fitness effects of inter-deme competition.

We are interested in the effect of variations in the fraction of a deme that are A's (p_j) on the probability that the deme will survive a contest (λ) or $\lambda_A \equiv d\lambda/dp_j$. For reasons of empirical and analytical tractability we seek a formulation in which this expression is invariant with respect to other aspects under study (in particular p_j). An example is $\lambda = z + (1-2z)p_j$ where $z \in [0, \frac{1}{2}]$. Using this function $\lambda_A = (1-2z)$ so the alternative assumptions used in the text are $\lambda_A = 1$ when $z = 0$ and $\lambda_A = \frac{1}{2}$ when $z = \frac{1}{4}$. When $z = \frac{1}{2}$ the faction of A's in the group has no effect on its survival probability. One can see from equation 6 that for given values of the other parameters and $F_{ST} < 1$ there exists a critical value $z^* < ½$ such that for values greater than z^* the A's cannot proliferate. This critical value is given (rearranging equation 6 and using $\lambda_A = (1 - 2z))$ by

(S12) $z^* = ½ - ((1-\tau)c/4\kappa)(1 - F_{ST})/F_{ST}$

The two terms on the right-hand side of (S12) capture, respectively, the ratio of individual costs to the deme benefits of altruism, and (inversely) the degree of genetic differentiation in the population. Using the benchmark parameters from Table 3 with $c = 0.02$ we have $z^* = 0.36$ so $\lambda_A = 0.28$. This means that for the benchmark parameters altruism could proliferate even if the effect of the fraction of altruists on the probability of survival were considerably lower than the lesser of the two benchmark values of λ_A used in the text.

With some restrictions we can derive an equally simple expression for λ_A from a model in which contests are explicit. The expected probability of deme j surviving a contest with deme q may be written

(S13) $\lambda = ½\{1+ \max(p_j - p_q, 0)^\mu - \max(p_q - p_j, 0)^\mu\}$

with $\mu \in [0,1]$. If $\mu = 1$ then we have a survival function $\lambda^1 \equiv ½(1 + p_j - p_q)$ for which $\lambda_A = ½$. If $\mu = 0$, λ takes the value of 0 if deme j has fewer A's, 1 if deme j has more A's and ½ if the two are equally matched. If p_q were uniformly distributed on the unit interval, $\mu = 0$ then gives a survival function $\lambda^0 = p_j$, so $\lambda_A = 1$ (There is no reason to expect this assumption to hold, it simply allows a comparison between the survival functions using S13.) If the p_q were bunched around some central tendency λ_A could greatly exceed 1.

[Figure S2 here]

To illustrate the difference between $\mu = 1$ and $\mu = 0$, the two models are compared in figure S2 (for p_q arbitrarily set at one-half). If $\mu \in (0,1)$ the survival function lies between the two, indicated by the dashed line (but then λ_A varies with p_j). One can see that if equation S13 is the correct survival function, then $\mu = 1$ (i.e. $\lambda_A = ½$) is a limiting case. This is because $\mu > 1$ ($\lambda_A < ½$) implies implausibly that the effect on the probability of survival associated with variations in the fraction of altruists in a deme (λ_A) is larger when p_j differs greatly from p_q than when the two demes are more similar. In figure S2, this is shown by the dashed line labeled $\mu > 1$ that is steep at the extremes and flat over intermediate values.Survival functions other than S12, however, allow values of λ_A less than ½ or greater than 1, so neither can be shown to be a limiting case.

However, setting $\mu = 1$ (that is, $\lambda_A = ½$) makes the influence of altruists on deme survival quite modest. Suppose that A's are willing to fight while N's do not participate in a conflict. Then $\lambda_A = ½$ gives a deme a positive probability of survival even if it has no fighters unless it is matched with deme in which every member is a fighter. And a deme all of whose members were prepared to fight when if paired with a deme only half of whose members were fighters, nonetheless would stand a one-in-four chance of perishing. Given the very low-technology nature of Pleistocene warfare, the fact that a two-to-one numerical advantage does not translate into a greater difference in the probability of victory indicates that $\lambda_A = ½$ implies a rather weak relationship between the fraction of A's and the probability of survival.

On the basis of their model, Boorman and Levitt (*4*) concluded that inter-demic selection would be of limited importance unless the survival function approximated a step function (as in the case of $\mu = 0$ i.e. $\lambda_A = 1$). The results (**A** panels of Figure 1 and left panels of FigureS5) show that this is not the case here.

Ideally we would determine the fitness consequences of deme competition from the demographic histories of a random sample of pre-contact hunter-gatherer groups. Even if such data were it available would be far from random (biased towards those who either avoided or won conflicts). We need to account for both differential mortality in conflicts and the associated territorial losses or gains. The available record contains few pre-contact histories of groups extending over more than a half a century. The best we can do is to make inferences from the available data, namely: what is known about hunter gatherer demographics, late Pleistocene climate records, archeological evidence on causes of deaths during the Pleistocene and ethnographic and historical reports on recent foragers.

Frequent catastrophic mortality (due to conflicts, environmental challenges and other causes) is the most plausible way to reconcile two pieces of evidence about hunter gatherer demography(*16*). First, human population grew extraordinarily slowly or not at all for the 100,000 years prior to 20,000 years before the present with estimated growth rates ranging from .002 percent per annum in the earlier period to 0.1 percent in the later (*17, 18*) Yet models and data on hunter gatherer demographics show that they are capable of growth rates in excess of 2 percent per annum (*19-21*)

Evidence of late Pleistocene climate variability is presented in Figure S3. Deep sea cores in the Western Mediterranean and other data suggest that the climate variability shown in the figure was a general northern hemisphere phenomenon (*22*). Surface temperature scales approximately linearly with the $\delta^{18}O$ signal shown in the figure. Differences in temperature (Centigrade) are about 1.2 times the difference in the signal shown the figure (*23*). Even these 50-year average smoothed data (shown here, to minimize spurious variation due to measurement error) indicate that changes in mean temperature as great as 8 degrees (C) occurred over time spans as short as two centuries. By way of comparison, the Little Ice Age that devastated parts of early modern Europe experienced a fall in average temperatures of one or two degrees, and the dramatic warming of the last century raised average temperatures by one degree, comparing the unprecedentedly hot 1990s with a century earlier (*24*) See also (*25*). In light of the climate record Boehm (*26*):19 writes that :

> .. towards the end of the Pleistocene as anatomically modern humans began to emerge, group extinction rates could have risen dramatically as needy bands of well armed hunters, strangers lacking established patterns of political interaction frequently collided, either locally or in the course of long distance migration.

A statistical analysis of recent ethnographic evidence is consistent with Boehm's conjecture. Carol and Melvin Ember (*27*)conclude that a " history of unpredictable natural disasters strongly predicts more war...people, particularly in nontate societies may try to protect themselves against future disasters by going to war to take resources from enemies."

[Figure S3 here]

The impact of climate variation is also suggested in the archaeological record. Commenting on a burial from 12-14,000 years ago in which almost half of the skeletons indicated a violent death, Wendorf (*28*):993 explained:

> Population pressures may have become too great with the deterioration of Late Pleistocene climate and the effects which this had on the herds of large savanna type animals which were the primary source of food at this time. ...a few localities which were particularly favorable for fishing would have been repeatedly fought over as sources of food became increasingly scarce.

Archeological evidence on Southern Californian maritime hunter-gatherers over a 7000 year period indicates that violent deaths occurred disproportionately during periods of climatic adversity and resource stress(*29*). The archeological evidence is summarized in Table S3.

[Table S3 here]

Drawing inferences about the frequency and intensity of group conflict from these data face three main problems. First, as with most archeological data, it is impossible to establish if the sites that have been studied are representative of late Pleistocene and early Holocene conditions. Second, many deaths in warfare do not leave projectile points embedded in bone or the other traces of violent death used in these studies, because "the most deadly injuries are those to the thorax and abdomen, wounds that often do not involve bone."(*29*):92 As a result most data are underestimates, a possibility mentioned by many of the authors (eg. (*28*):993) and judged to be significant in magnitude in one case: "an analysis that included only projectile points embedded in bone would miss over half of the projectiles ... and 75% of what was in all probability the actual number of projectile wounds." (*29*):93 Third, while some burial evidence is suggestive of ongoing intergroup violence (simultaneous burials and healed forearm injuries, for example) one cannot readily distinguish between deaths due to intergroup violence that occurring within groups.

The average fraction all deaths due to violence of the sites in Table S3 is 13.1 percent. This compares with estimates well below one percent of male deaths for Europe and the U.S. in the 20th century, three percent of all deaths for 19th century France and 0.02 of all deaths for Western Europe in the 17th century, a period of virtually continuous conflict (*30*). But it is considerably below the 33.5 percent al all deaths due to warfare estimated from ethnographic data for the pre-contact (before 1970) Ache in Paraguay (*31*).

Ethnographic studies of intergroup conflict allow estimates of the annual deaths due to warfare, averaging one-half of one percent for the 7 hunter gatherer reported in (*30*):195. This may be compared with the archeological evidence above: assuming a demographically plausible generation length (25 years). In this case four percent of the population dies annually so the ethnographic estimate indicates that 12.25 percent (= 0.005/0.04) of deaths are due to warfare. Including the Ache data just mentioned (not in the sample in (*30*)) raises the average to 14.9 percent.

Extensive ethnographic evidence shows frequent and lethal group conflict in many forager societies (*30, 32*). A study of Western American Indians found that four or more offensive or defensive raids took place annually in 43 percent of the 157 groups while only 13 percent experienced none or one raid (*33*). Table S4 summarizes the available surveys. These data may understate the extent of group conflict in the Pleistocene and early Holocene because some of the communities shown to make war rarely or not at all are under the administration of modern nation states or have suffered defeat in war and consequent subjugation by other dominant (non-state) groups. In these data sets there is no significant correlation of warfare with with population density, food storage, hierarchical political structure, and degree of inter-group mobility (*30, 32, 34*).

[Table S4 here]

Wars were especially lethal for the losers. None of the groups for which we have estimates of battle deaths for winners and losers are foragers, so we must rely on evidence from tribal and other pre-state conflicts. When the badly outnumbered Butelezi in Southern Africa succumbed to the Mtetwa-Zulu in 1810, they lost 8 percent of those engaged, while the Zulu lost only 1 percent ((*30*) p. 194). When the same Zulu group defeated the much larger Ndnandwe force three years later, the winners lost 8 percent of those engaged, but one in five of the losers perished. Battle deaths among the losing Dinka people during the mid-nineteenth century Nuer expansion into their territory amounted to 2.7 percent of the population annually, while population losses resulting from the capture of livestock increased this figure significantly ((*35*):61). Among the Mae Enga, collateral mortalities were also significant. Meggitt (*36*):112.) writes of

> the sudden and forced movements of women and children, the elderly and the ill, over difficult terrain in bleak and often wet weather. We simply do not know how many infants and old people succumb to pneumonia in these flights, how many refugees are drowned when trying to cross boulder strewn torrents, how many sick and weak people die because food supplies are interrupted. These less obvious costs of war...accumulate significantly through time..

Thus it seems likely that in the relevant periods of human history wars may have been frequent and they may have been quite lethal. How are we to estimate the fitness advantage of the winners? There are cases in the ethnographic record of virtually all members of a band being killed in a single decisive conflict, as when in 1849 a group of 52 Assiniboin encountered a much larger Blackfoot war party and was annihilated. ((*30*):194). But much more common are accounts of on-going low-level conflicts in which a few fatalities occur. Losing a conflict may reduce reproductive success in two ways: those killed in conflict leave no or fewer offspring; and those who survive the conflict may have reduced reproductive success either because they are displaced to less favorable environments, or they are assimilated by the winners or some other group in which they occupy socially inferior positions, at least for a few generations. Keeley (*30*):198 reports the percentage gains or losses of territory among five hunter-gatherer groups (Walbiri, Ingalik, Wappo, Kutchin, and Comox) averaging 16 percent per 25 years (gains and losses among pastoralists and horticulturalists are considerably greater).

Suppose groups compete in every generation and one group is the winner, the other the loser, and further that due to the carrying capacity of the sites they jointly occupy, the change in population from one generation to the next is the proportional to change in territory each commands minus the losses due to conflict. If (on the basis of the above estimates) we estimate that those lost in combat represent 0.005 of the adult population per year, that deaths are four times as numerous among losers as among winners, and that groups are initially of the same size, then losers lose 0.008 of their population from warfare annually, and winners lose 0.002. Ignoring the possibly considerable indirect loss of life among the losers due to hazardous relocation or subjugation by winners, and abstracting from territorial losses and gains, the winners would thus lose 5 percent per (25-year) generation and the losers would lose 22 percent.

What would be the impact on expected deme size of these contests taking place every generation? Let δ be the difference in expected deme size conditional on the deme being a winner or loser. Using the above data we estimate δ under two assumptions: δ^0 includes both the change in territory and the mortalities occasioned by the conflict, while δ^1 takes account of territorial changes only. In the first case the expected size of the winning deme after a generation (25 years) is (1.15)(0.95) and of the losing deme is (0.85)(0.78) so the difference, $\delta^0 = 0.43$. Ignoring wartime mortality differences the same calculation $\delta^1 = 0.3$. A contest that creates a per-generation difference in expected deme size of δ conditional on winning or losing is equivalent to a contest resulting in either the elimination or doubling of the deme occurring each generation with probability $\delta/2$, which is thus our estimates of κ (namely, 0.215 and 0.15, the latter ignoring wartime deaths) This suggests that continuous low level conflict might have effects similar to a single decisive conflict (the losers being annihilated the winning deme doubling in size) occurring at the rate of once every 4.7 (= 1/0.215) or 6.7 (= 1/0.15) generations. Figure 1 is based on the lesser of the two estimates of κ (rounded), such that decisive conflicts take place every 7 generations (i.e. $\kappa = 0.142$).

5. *Selection within demes*.

The appropriate value of n is the number of deme members of a breeding generation (about a third of the census size (*37*)). The median band (census) size among the 235 hunter gather groups recorded in (*38*)) is 19.

Studies of the Ache while foraging indicate that depending on the type of food, between half and ninety percent of food items are consumed by others but not the spouse, parents or children of the person who acquired the food (*39*). Weighting the food items by the share of total consumed calories constituted by each, the average sharing rate is 77 percent.. Using unpublished data from other hunter-gatherers supplied by Michael Gurven (Ache, forest Yora, Pilaga,Aka and Hiwi) the average sharing rate is 76 percent. Because data on food sharing may be more likely to be collected in societies in which this is commonly done, I select a somewhat lower figure, $\tau = 0.66$, as the benchmark value and $\tau = 0.33$ as an alternative.

For non-human organisms selection coefficients have been measured by experimental methods. Estimates of the fitness effects of both deleterious and advantageous mutations in *Drosophila melanogaster, E. coli*, and *S. cerevisiae* suggest selection coefficients of about 0.02 or less (*40-43*). However some estimates of selection coefficients in the wild are considerably larger than this (*44*).

The change in the frequency of the A trait in deme j is proportional to $p_j(1-p_j)$ because the (discrete time) replicator equation giving the change in the frequency of A's in deme j is

(S14) $$\Delta p_j = - p_j(1-p_j)(1-\tau)c$$

Equation S14 suggests that if an adverse climate shock or some other disturbance induced a period of hostilities followed by site repopulation and deme fission had propelled a few surviving demes to high frequencies of altruism, a substantial fraction of A's in the total population could then persist over a long period during less competitive times. The reason is that the pace at which A's are replaced by N's reaches a maximum at $p_j = ½$ and becomes vanishingly small as p_j approaches 1. Thus once having obtained a high fraction of As, a deme will replace A's by N's initially at a very slow rate.

6. Dynamics of an F_{st} at a locus under directional selection

Despite the fact that an altruistic allele would be under directional selection, high levels of F_{ST} could be maintained over long periods. To see this consider the following example: the population has two demes; 90 percent of one are A’s while the other is evenly split. Equation 14 shows that both demes are expected to have fewer A’s the next period. But (also by equation S14) selection against the A's in the evenly divided deme (proportional to $p_j(1-p_j)$) will be much stronger (two and a half times) than in the predominantly A deme, so the means of the two demes will diverge, driving up the between-deme variance. (The within-deme variance of the second deme will fall, while that of the first deme will rise.)

To determine the net effect of these changes we use equation S14 (assuming $\tau = 0$) to calculate the next period distribution of A’s in each of 9 demes. From these we then calculate the within- and between-deme variances and then repeat this process over hundreds of generations. There are no other influences on the evolution of the p_j (no matching noise, no deme extinctions, no deme fission, no other stochastic events). The trend in the F_{st} depends on the initial distribution of the p_j. As the mechanism at work in above two-deme example suggests, if no deme is above the mean, both the within- and between-deme variance must fall over time. The former occurs because the within-deme variance is at a maximum at $p_j = 0.5$ and p_j will be falling in every deme. Between-deme variance falls because the selection pressure on the As in the high p_j demes will exceed that in the low p_j demes, reducing the between-deme variance. But as Figure S4 shows, for a wide variety of initial distributions the F_{st} rises initially and then declines.

The right hand graphs are perhaps the most relevant to the initial emergence of altruism, for they describe a case in which a deme of closely related A's (by chance or design) form a single propagule (as the result of a tribe-splitting) in a population with few other A's. Once established in a small number of demes, a substantial level of p could be sustained in the entire population and the long term trend of F_{st} might resemble the graphs on the left with occasional 'resets' to one of the initial seeds due to group extinction, site repopulation, and fission.

[Figure S4 here]

7. *Relaxing the carrying capacity constraint*

Relaxing the absolute constraint on deme growth in the absence of territorial expansion may be studied by assuming that a deme may contribute more members to the next generation both by exporting migrants or by acquiring and repopulating new sites upon surviving a contest(but not in both ways in a given period). This would require that unsaturated sites are available for migrants from the deme and that should the deme survive a contest the vacated site of the losers will be repopulated by the surviving deme. To model this process we add a selective emigration model (*7*) to the selective extinction model. In the absence of a contest and with no constraints of population growth, a deme contributes $(1 + p_j(b - c)$ to the next generation. We introduce less than complete saturation by expressing expected deme size in the absence of conflict as $(1 + gp_j(b - c)$ where $g \in [0,1]$ is an inverse measure of the degree of density dependent regulation. When $g = 1$ the deme is unrestricted in exporting population, while $g = 0$ gives the absolute density saturation limit modeled in the text whereby a deme may expand its population only by acquiring a new site.

As before, the expected size of the deme is $\lambda 2$ if a conflict occurs. Adding the two expected sizes, weighted by the probability of a conflict, κ, we have $w_j = \kappa\lambda 2 + (1-\kappa)(1 + gp_j(b - c))$, the derivative of which with respect to p_j is $\kappa 2\lambda_A + (1-\kappa)g(b-c)$. So the equivalent of equation 6 becomes:

(S15) $$F_{ST}/(1-F_{ST}) > (1-\tau)c/\{(1-\kappa)g(b-c) + \kappa 2\lambda_A\}$$

Relaxing the carrying capacity constraint (higher values of g) renders the condition for the evolution of altruism less stringent. (Equation 5 is modified in exactly the same manner).

8. Conditions for the evolution of altruism for 6 forager-based estimates of F_{st}

[Figure S5 here]

9. Figures (following pages)

Figure S1. Hierarchical measures of genetic differentiation. The arrows indicate the units among which genetic differentiation is measured by the given F-statistic

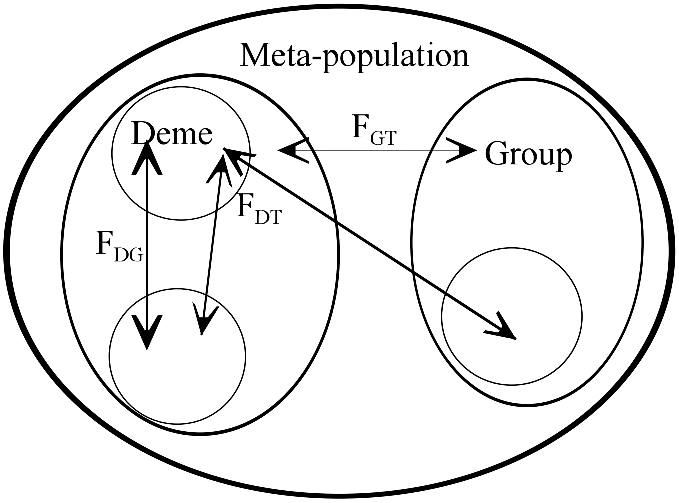


Figure S2. Survival probability for deme j if half of the paired deme are A's. The linear function is λ^1 ($\mu = 1$); the step function is λ^0 ($\mu = 0$). Varying p_q shifts the first function vertically without changing its slope (½) and shifts the vertical dashed line horizontally so that if p_q is uniformly distributed over the unit interval $\lambda_A = 1$. The dashed line labeled $0<\mu<1$ is an intermediate function.

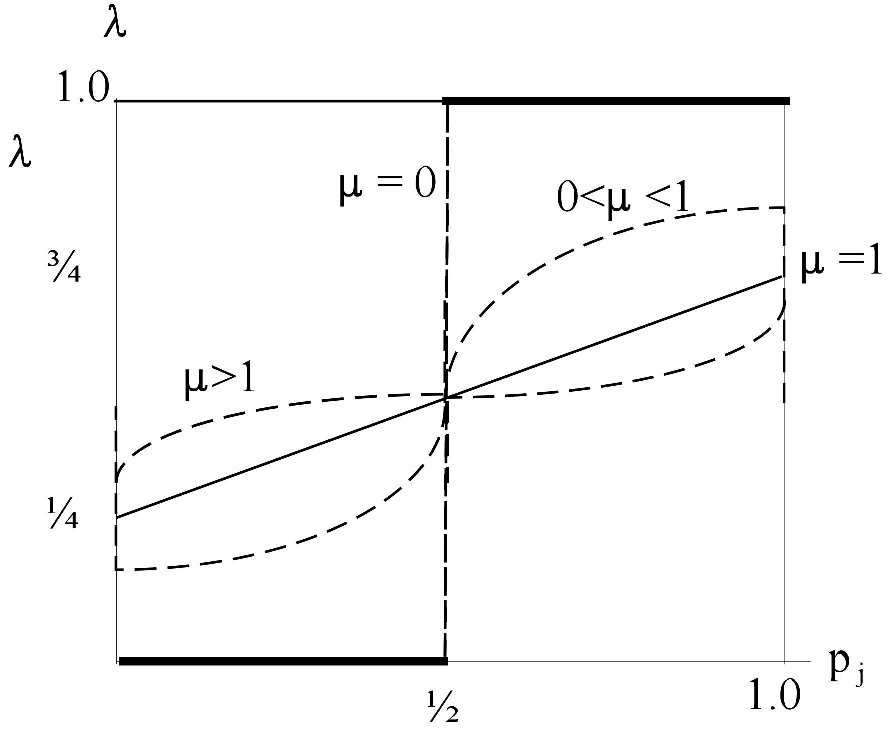


Figure S3. Pleistocene temperature variations Shown are measures of δ^{18} O taken from Greenland ice cores (from http://www.glaciology.gfy.ku.dk/ngrip/index_eng.htm and described in (*45*))

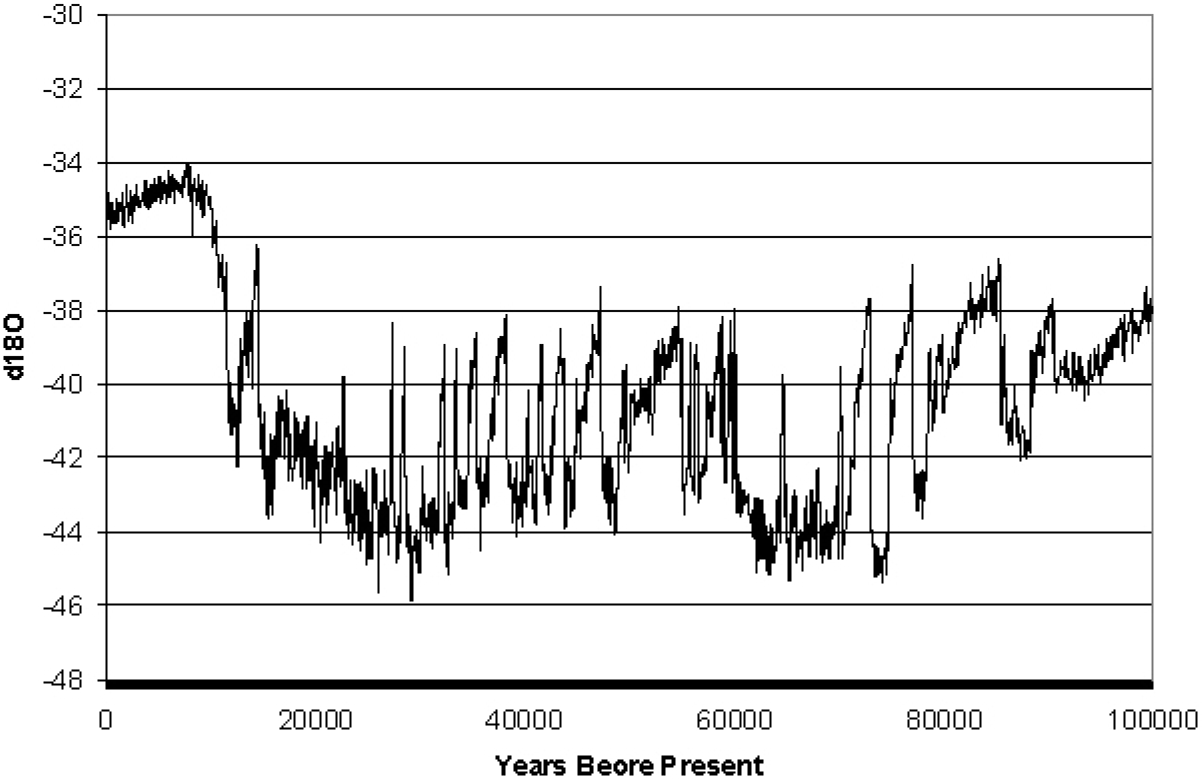
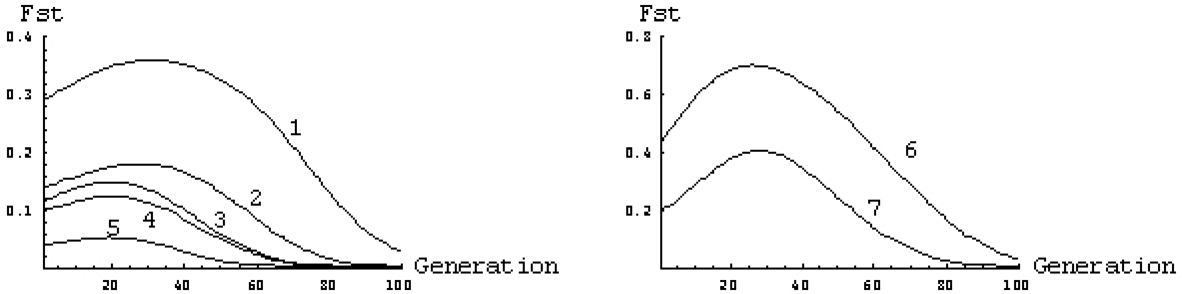


Figure S4. Dynamics of an F_{st} at a locus under directional selection . Selection against the altruistic allele is given by $-c$ where $c = 0.02$ in the top panel and $c = 0.1$ in the bottom panel. The original distribution of altruists in nine demes is indicated by the numeric labels in the figure. **1**:{0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9}, **2**:{0.2, 0.3, 0.4, 0.5, 0.5, 0.5, 0.6, 0.7, 0.8}, **3**:{0.3, 0.3, 0.3, 0.5, 0.5, 0.5, 0.7, 0.7, 0.7}, **4**:{0.3, 0.3, 0.4, 0.4, 0.5, 0.6, 0.6, 0.7, 0.7}, **5**: {0.4, 0.4, 0.4, 0.4, 0.5, 0.6, 0.6, 0.6, 0.6}, **6**:{0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.1, 0.9}, **7**:{0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.2, 0.8}

(a) c = 0.02



(b) c = 0.01

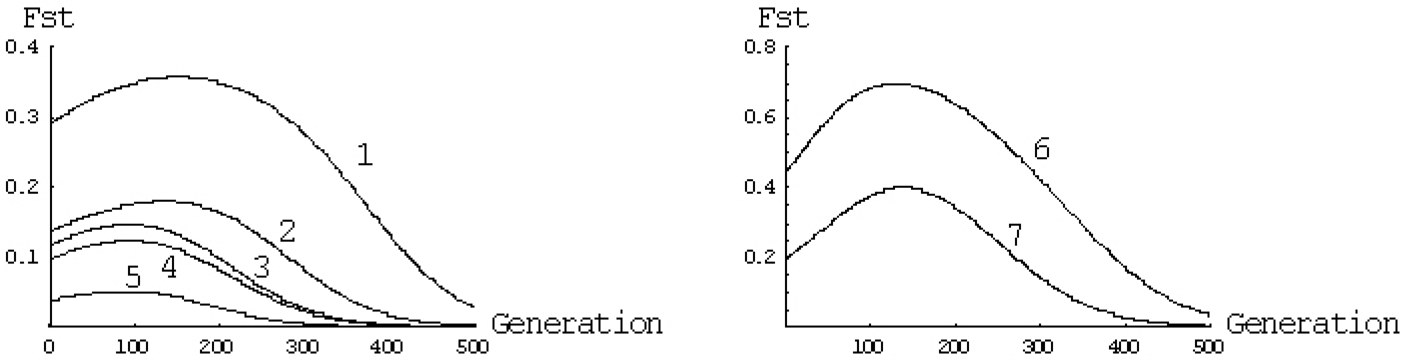
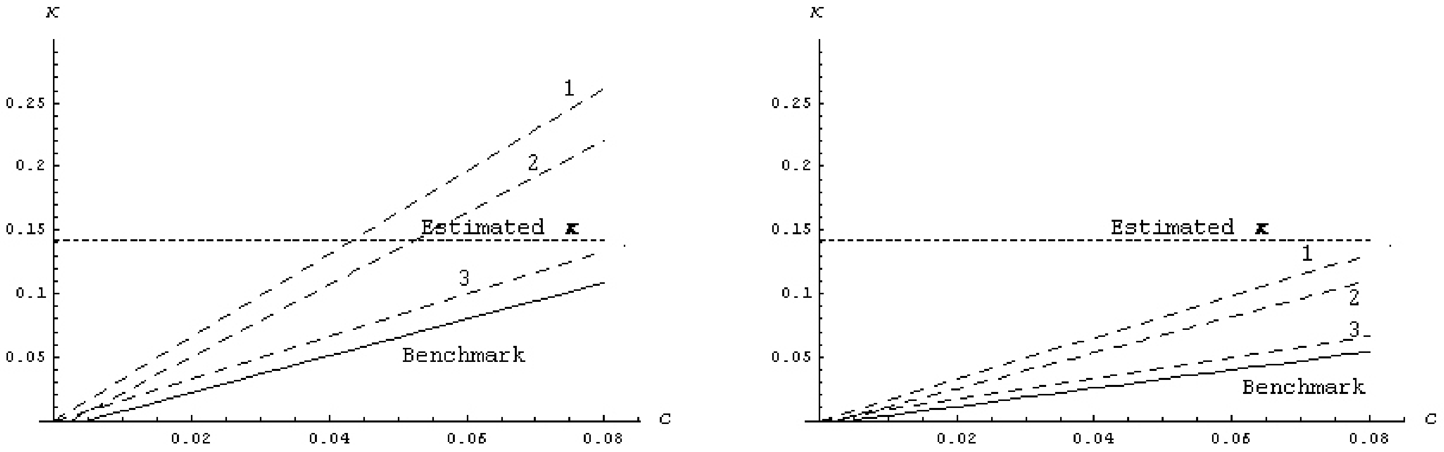
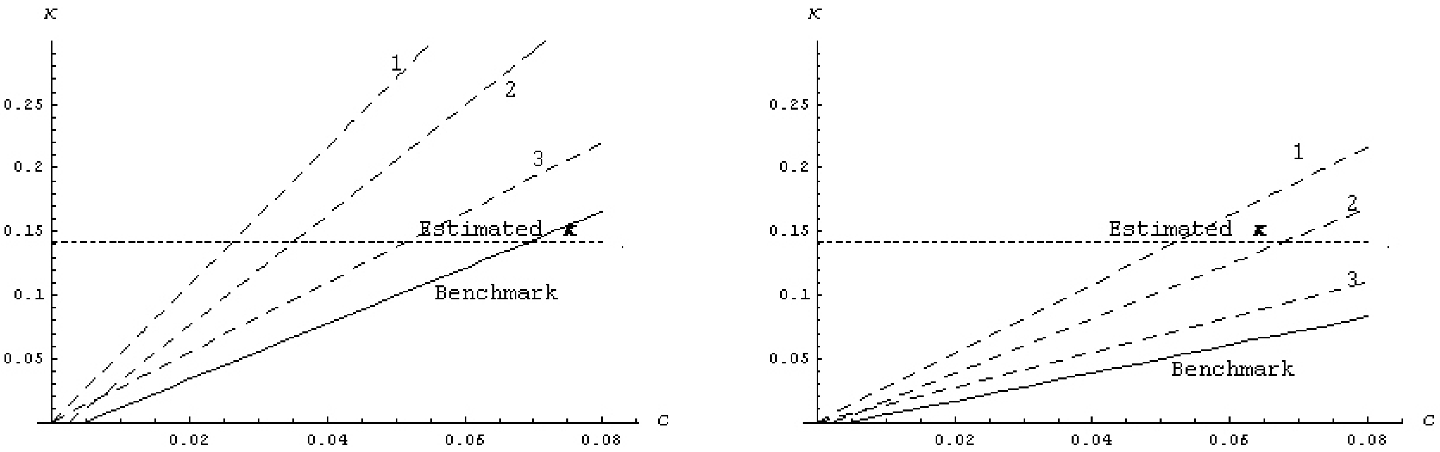


Figure S5. Conditions for the evolution of altruism. The figure is identical to Figure 1 except that estimates of F are from the societies indicated excluding the median group in Table 4 (one of the circumpolar groups = 0.076) and the Southern African groups (because their F-value is virtually identical = 0.075. The San-Mbuti F-value is also not used as it is very close to the Native Siberian populations show in figure S5a. The solid lines in the left panel give the values of c and κ that satisfy equation 5 as an equality, using the benchmark values estimated in the text n=32, τ=0.66. Thus points above the sold line give combinations of c and κ such that altruism would proliferate according to equation 5. Dashed lines give similar information for differing group size and extent of reproductive leveling. Line 1: $n=\infty$, τ=0.33; Line 2: n=32, τ=0.33 Line 3: $n=\infty$, τ=0.66The left and right panel are for (respectively) $\lambda_A = ½$ and $\lambda_A =$ 1.For both panels, b=0.05.

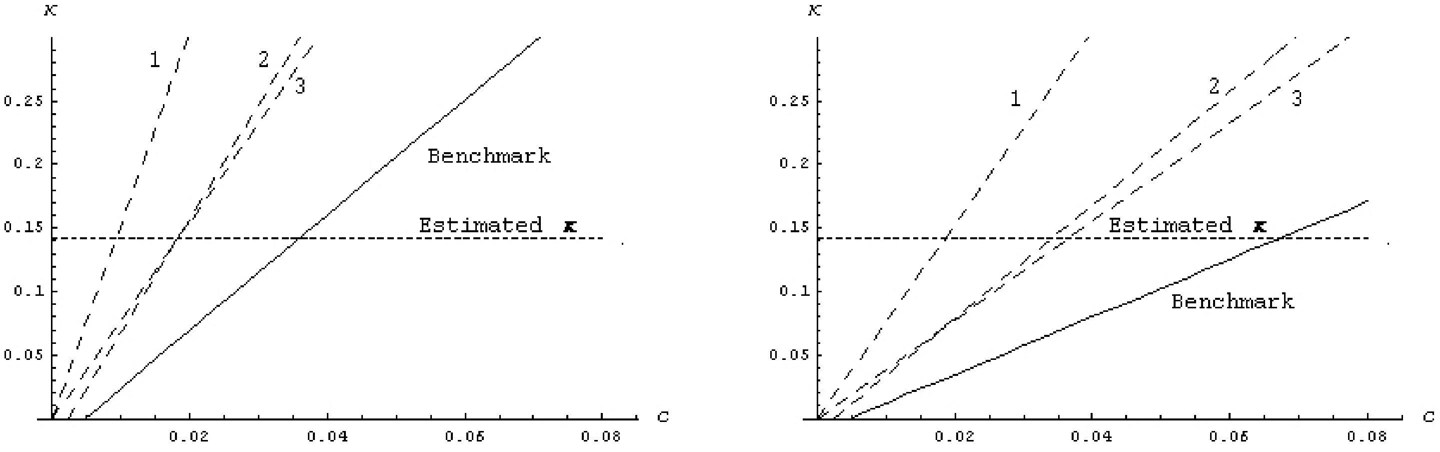
(a) Native Siberian populations (F_{DT}=0.17)



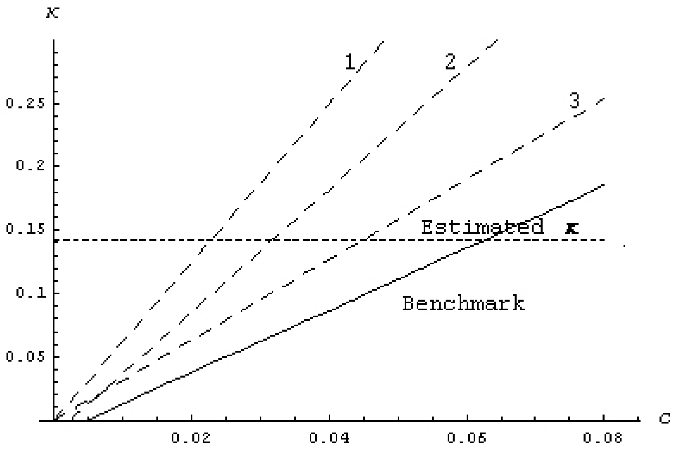
(b) Native Siberian (within group) (F=0.11)

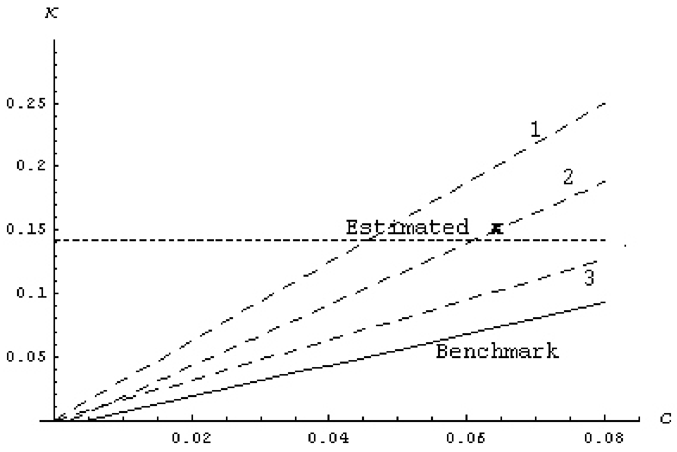


(c) Aka (between ‘villages’ in the same group) Aboriginal Australians (F = 0.042)

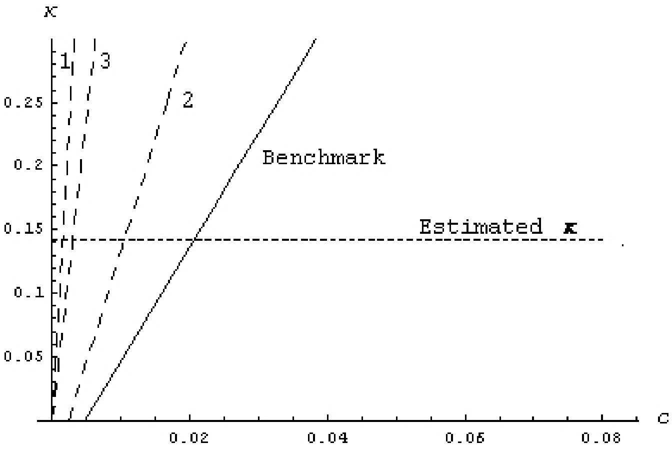


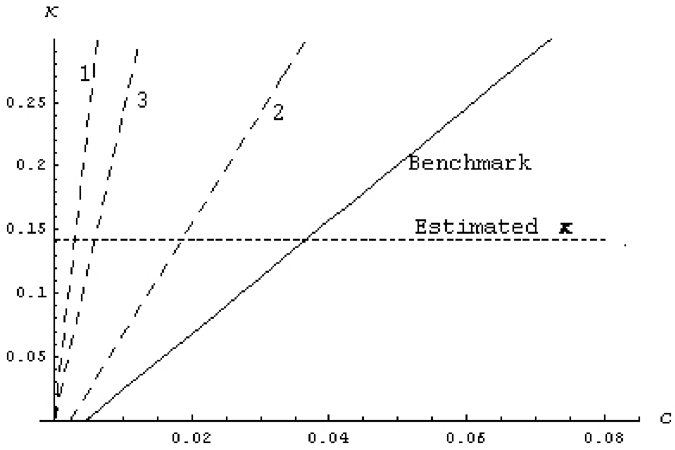
(d) Aka (between ‘villages’ in all groups) (F_{DT}=0.097)



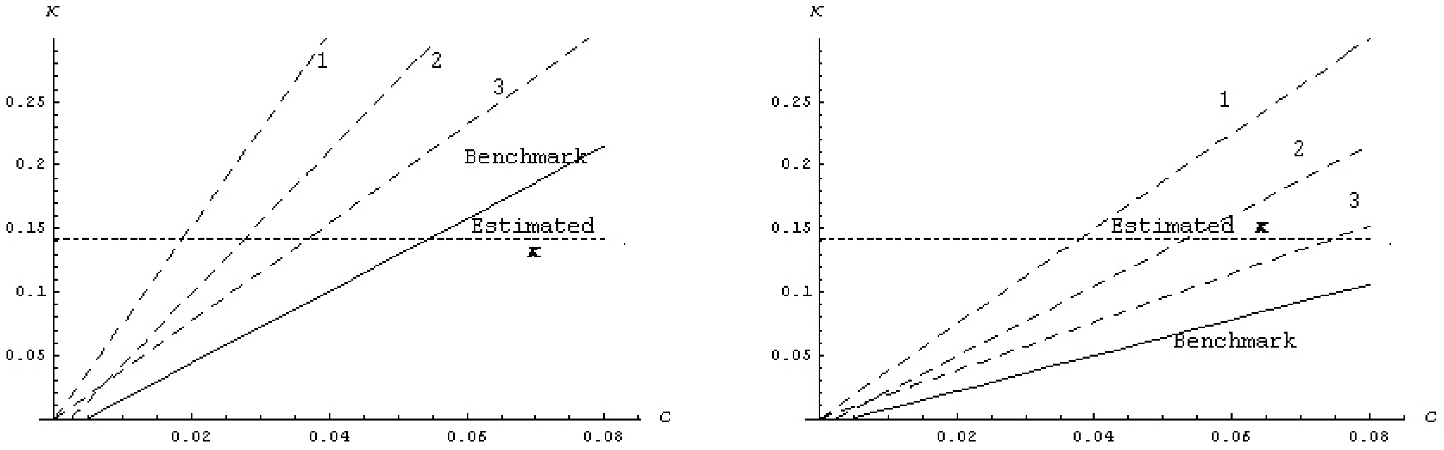


e) !Kung (F_{DG}=0.007)

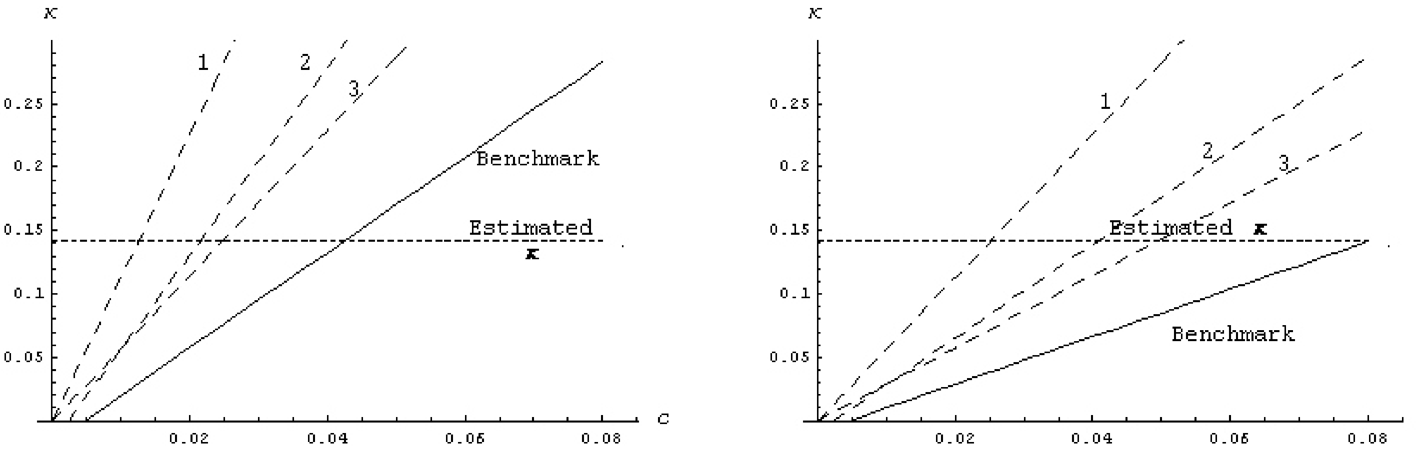




(f) SAfrican demes and Kaiadilt-Lardiil (Aus) (F_{DT}=0.081)



g. Asmat-Mappi (Western New Guinea) (F_{DT}=0.056)



10. Tables

Table S1: Associative tribe-splitting

Seceding head is	Prob	p_A of daughter deme	p_A of remaining deme
A	p	$r + (1-r)p$	$2p - r-(1-r)p$
N	$1-p$	$p - rp$	$2p - p + rp$

Table S2: Sources, methods and background for the estimates in Table 4

Population: date genetic material collected (source)	*Social, economic and demographic characteristics*	*Method of estimation*
Indigenous circumpolar Eurasian: 1950s-1960s (*46*)	Descendants of hunters of the Late Pleistocene in 58 semi-isolated demes from 16 ethno-linguistic groups; exogamous marriages 15 percent	p.70 s.e. of estimate is ± 0.013
Native Siberian populations : various (*47*)	18 "traditional settlements' whose 'traditional Siberian life ways reflect common features of hunter gatherer existence..' Highly differentiated groups in close proximity.	Table 3, p775. Φ_{ST} =0.45 (among demes in meta- population), autosomal equivalent approximated by equilibrium $\phi^* = 1/(1+nm)$ and using the implied value of *nm* in $F^* = 1/(1+4nm)$ (no s.e. given)
Native Siberian populations: various (*47*)	Immediately above	p 774 Φ_{SC} = 0.34 (demes in a language group) converted to autosomal equivalent as above. (no s.e. given)
!Kung: 1960s (*48*)	Six subpopulations of 'pure !Kung' among whom there were 'no perceptile clustering of social or breeding relatins into isolates or semi-isolates'; very high migration.	p.154 Corrected for sampling bias. (no s.e. given)
Southern African groups: 1960s (*49*)	18 populations in different language groups, substantial admixture among groups.	Average diagonal entries in table 29 (p. 193 see also p. 189). The mean reported in the source (p. 194) is in error.(± 0.067)
Southern African demes: (from 18 groups):1960s	Immediately above	Using $F_{DT} = F_{DG} + F_{GT} - F_{GT}F_{DG}$ from above estimates (*48, 49*)
Aboriginal Australians: 1960s (*50*)	Range expansions populated the continent, foraging persisted until European contact; 15 percent of marriages outside of (small) dialect groups	Average of the diagonal elements ϕ_{ii} in table 2 p. 326. (± 0.025)

Kaiadilt-Lardiil groups (Australia): 1940s (*51*)	Adjacent dialect groups, genetic material collected virtually at contact, Kaiadilt suffered a major crash	Mean estimate calculated from from the ABO and Rh frequencies (tables 1 and 3 pp. 308,310) equal population weights. (± 0.003)
Asmat-Mappi (New Guinea):1990s (*52*)	Lowland foragers in West New Guinea; very small (n=46) sample	Unpublished data on mitochondrial DNA converted to autosomal equivalent as above. Forager identification from (*53*)
Aka (between 'villages' in the same group) 1967-71(*54*)	From all individuals in about one-third of the Aka camps in the Central African Republic; long term close relations (and gene flow) with Bantu farmers	Mean of method 8 between villages of the same group, Table 23.4 p. 329 (± 0.041)
Aka (between groups): 1967-71(*54*)	Data from Aka in CAR (ave. of 4 sites), Zaire, & Cameroun	Computed from “angular distances”= d in table 23.5 p 330 with $F=4(1-\cos\theta)$ ((*37*) p 706) and $d=(1-\cos\theta)^{½}(2(2^{½}))/\pi))$ (from(*55*)), so $F=4d^2(\pi^2/8)$ (± 0.034)
Aka (villages in meta pop): 1967-1971 (*54*)	As above	Using $F_{DT} = F_{DG} + F_{GT} - F_{GT}F_{DG}$ and above estimates
Mbuti (Aka)-San various (*56*)	Comparison of an Aka group with San (Southern African).	p.75 Table entries for these F_{GT} and their standard errors are reversed in error (personal communication. from L.L.Cavalli-Sforza)

Table S3 Fraction deaths due to war: archeological evidence I have included British Columbia and Southern California data for all relevant periods and geographical areas and averaged the data from the Qadan burial with that of Jabel Sahaba, resulting in substantially lower estimates that reported in (*30*).

Site (source)	Date	%	
N. British Columbia(*57*)	3500BC-1774AD	21.8	Incl North and South, all dates
Nubia (*28*)	12,000 ybp	24.1	Adults (site 117 and 'Qadan')
Ukraine (Vasylivka) (*58*)	Mesolithic	15.9	Based on (*59*)
S. California(*29*)	3500BC-1380AD	7.5	Excluding later 'chiefdom'
Central California (*60*)	1500BC-500AD	≥5.0	Points embedded in bone only p183
Denmark (Vedbaek) (*61*)	4100BC	13.6	“affluent foragers”
Sweden (Sketeholm I) (*61*)	4300BC	≥3.8	Points embedded only

Table S4. Warfare in hunter-gatherer societies Note: The table shows the percent of all N groups with each degree of frequency of warfare. Continuous is defined as (for row 1) "constant" meaning "annual"; (For row 2): both internal or external warfare occurs 'at least every five years,' and one of these occurs "at least yearly"; and (for row 3) "more than once every two years."

Source	Continuous	Frequent	Rare	N	Comment
Otterbein (*62*)	20	50	30	10	"constant"
Kelly (*32*), based on Ross (*63*)	24	48	28	25	external and internal
Ember (*64*)	65	25	10	31	including ambush

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