Supporting online materials for

Group competition, reproductive leveling and the evolution of human altruism

Samuel Bowles, Santa Fe Institute and Universitá di Siena

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

or, upon rearranging,

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

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

(S5) $$\mathrm{var}(p_j;\, r, \infty) = p[\{r+(1-r)p - p\}^2 + \{2p - r - (1-r)p - p\}^2]/2$$

$$+ (1 - p)[(p - rp - p)^2 + (2p - p + rp - p)^2]/2$$

$$= p(r-rp)^2 + (1-p)(-rp)^2 = p(1-p)r^2$$

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

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

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:

(S7) $$n^*(r) = 1/r^2$$

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 $z \in [0, ½]$. Using this function $\lambda_A = (1-2z)$ so the alternative assumptions used in the text are $\lambda_A = 1$ when $z = 0$ and $\lambda_A = ½$ when $z = ¼$. When $z = ½$ 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

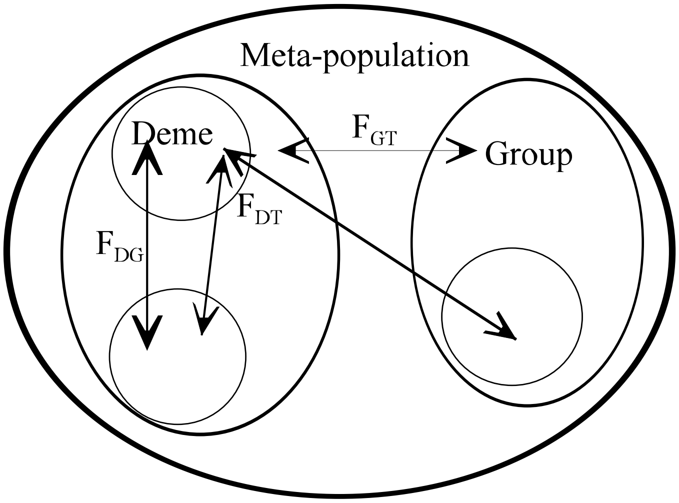


Figure S2. Survival probability for deme j if half of the paired deme are A's. The linear function is λ^1 ($\mu = 1$); the step function is λ^0 ($\mu = 0$). Varying p_q shifts the first function vertically without changing its slope (½) and shifts the vertical dashed line horizontally so that if p_q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

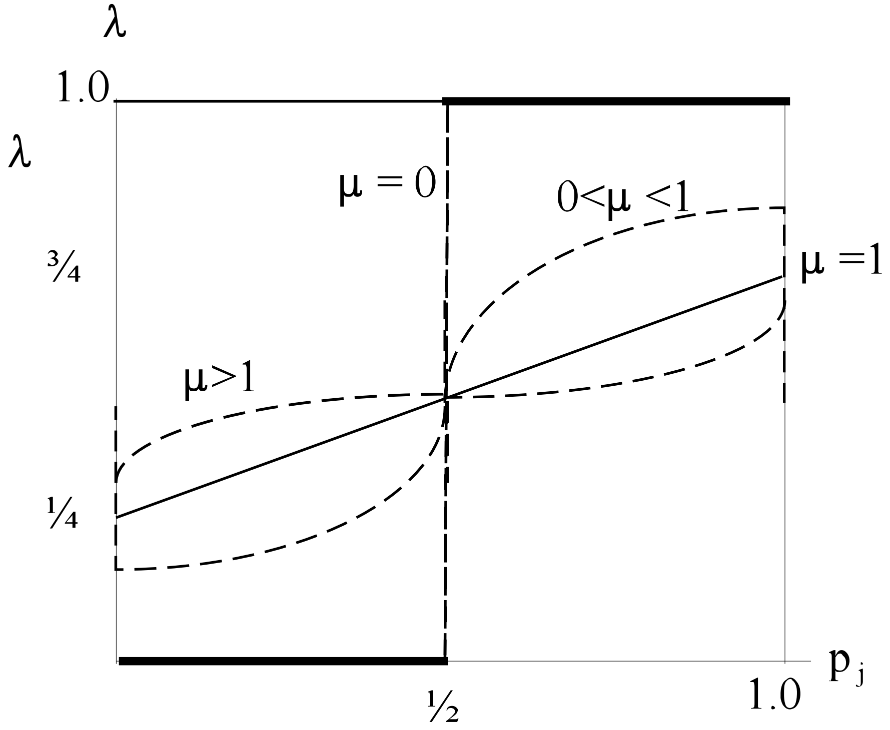


Figure S3. Pleistocene temperature variations Shown are measures of δ^{18} O taken from Greenland ice cores (from http://www.glaciology.gfy.ku.dk/ngrip/index_eng.htm and described in (*45*))

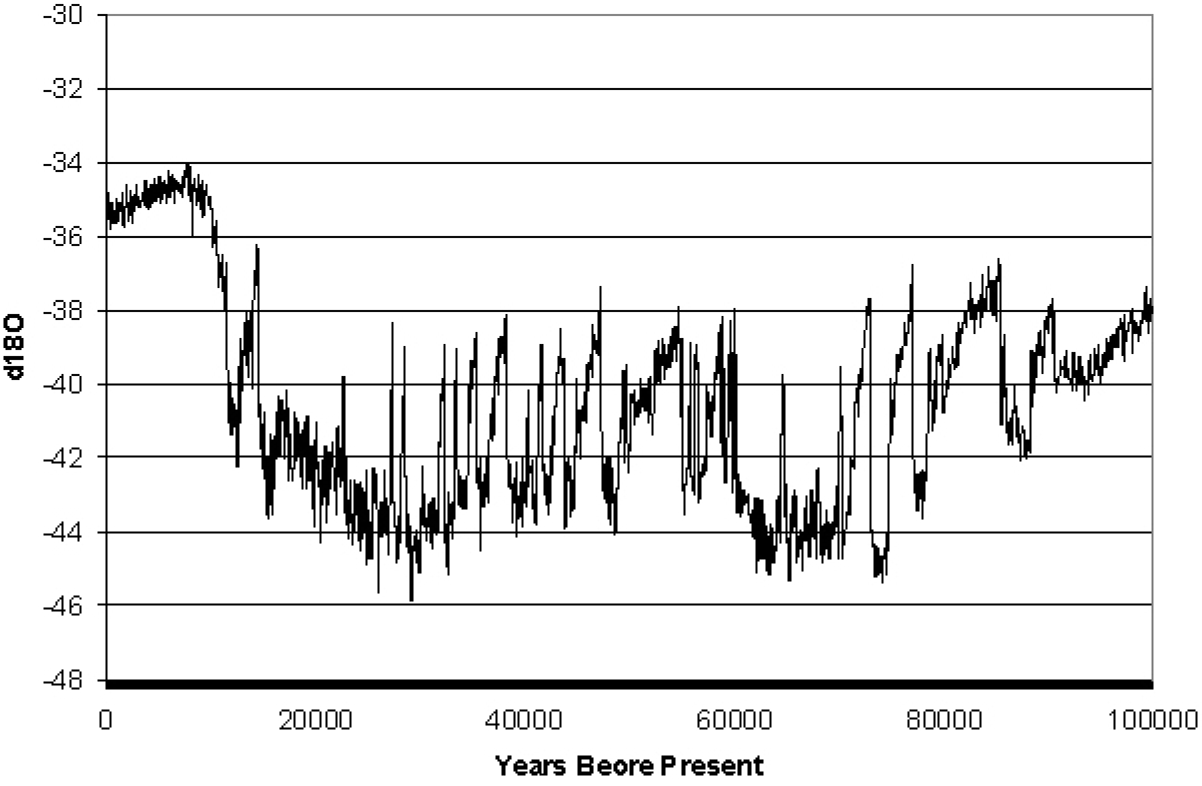
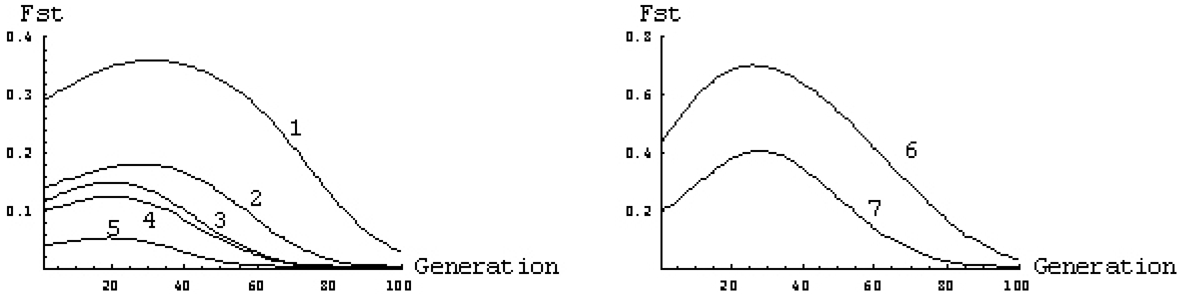


Figure S4. Dynamics of an F_{st} at a locus under directional selection . Selection against the altruistic allele is given by – *c* where *c* = 0.02 in the top panel and *c* = 0.1 in the bottom panel. The original distribution of altruists in nine demes is indicated by the numeric labels in the figure. **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

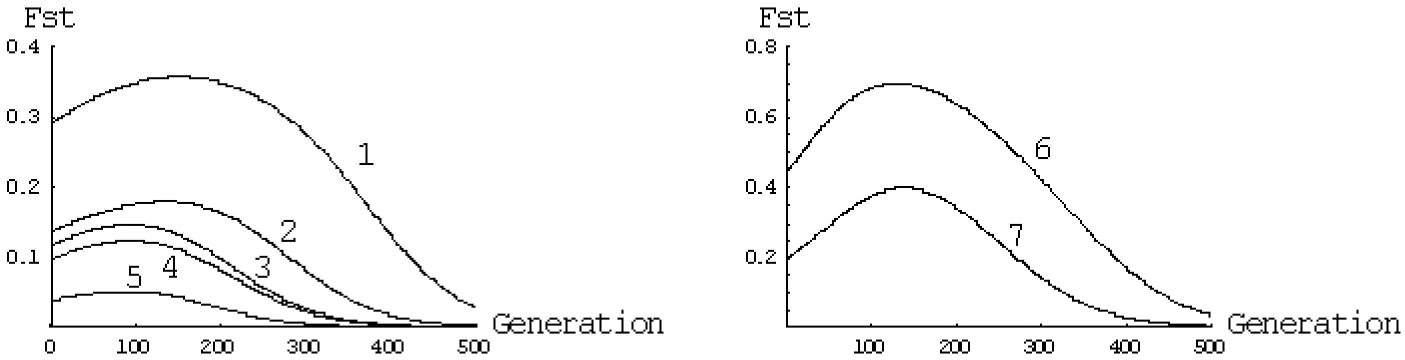
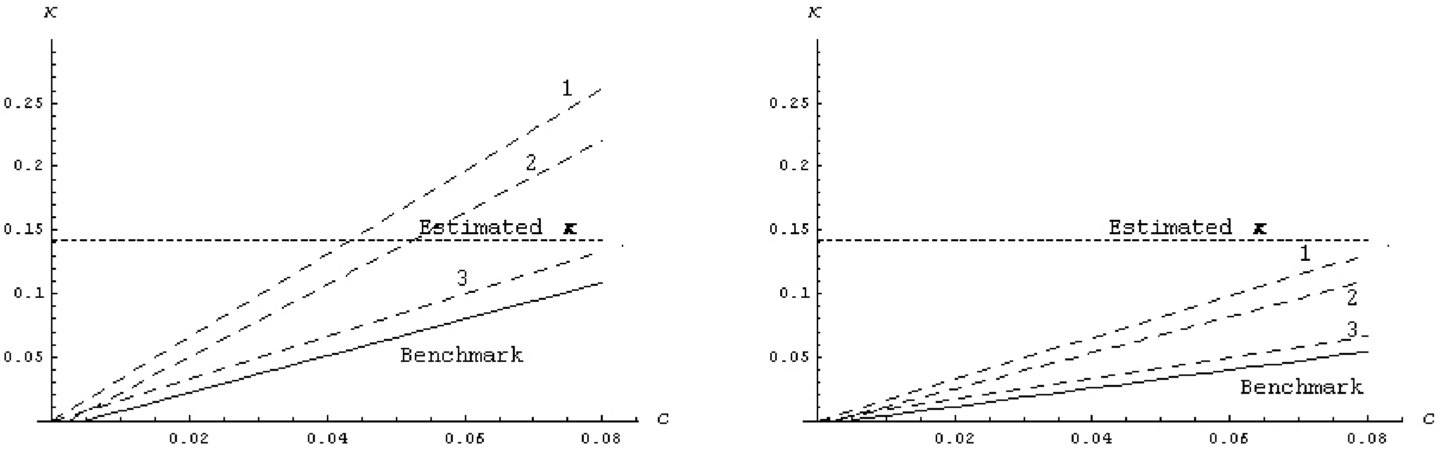
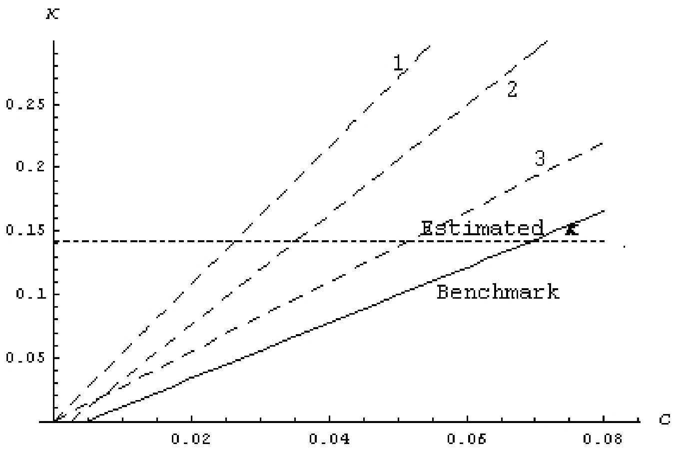


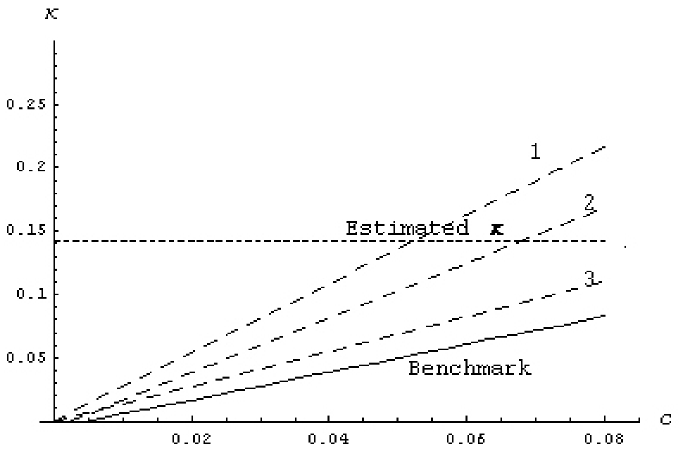
Figure S5. Conditions for the evolution of altruism. The figure is identical to Figure 1 except that estimates of F are from the societies indicated excluding the median group in Table 4 (one of the circumpolar groups = 0.076) and the Southern African groups (because their F-value is virtually identical = 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) λ_A = ½ and λ_A = 1.For both panels, b=0.05.

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

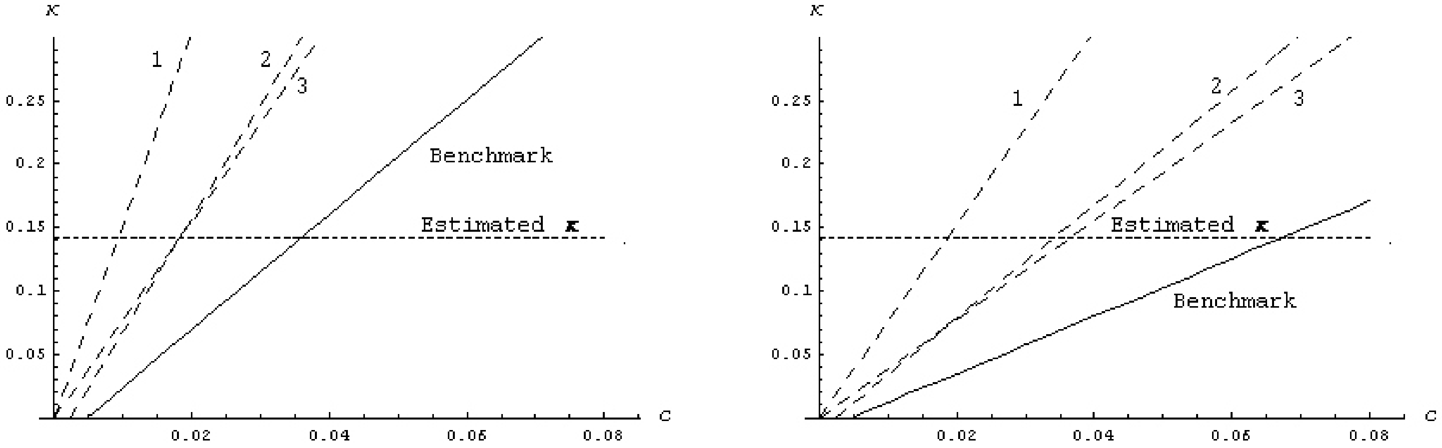


(b) Native Siberian (within group) (F=0.11)

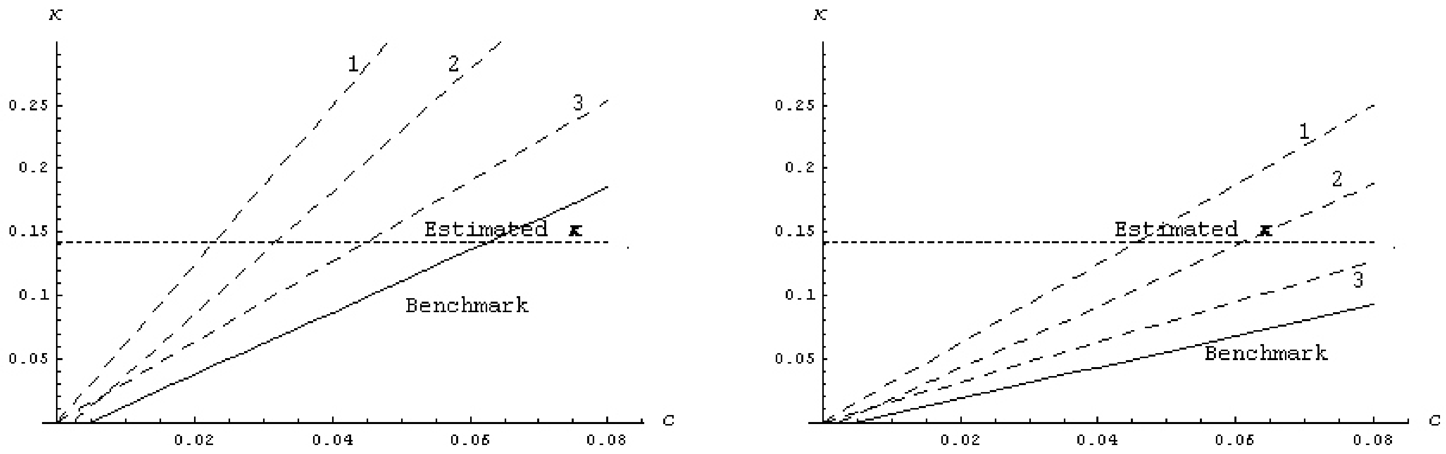




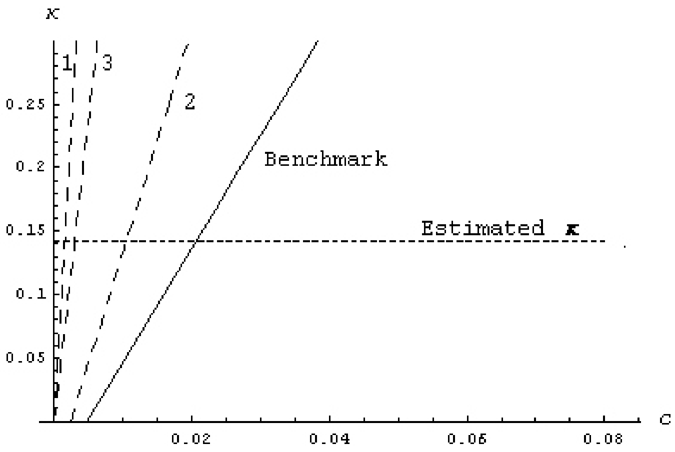
(c) Aka (between ‘villages’ in the same group) Aboriginal Australians (F = 0.042)

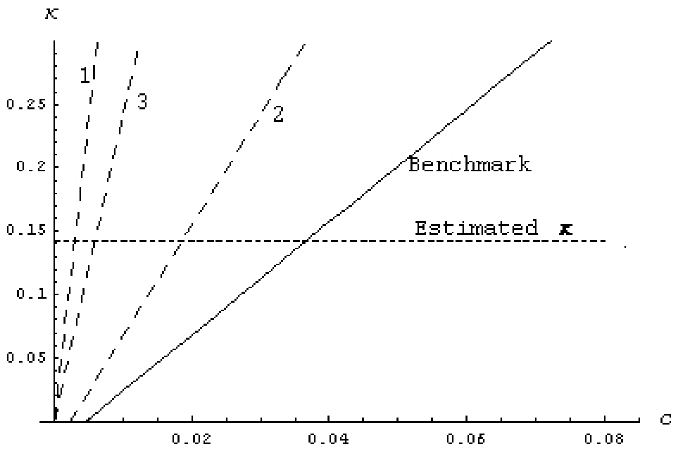


(d) Aka (between ‘villages’ in all groups) (F_{DT}=0.097)

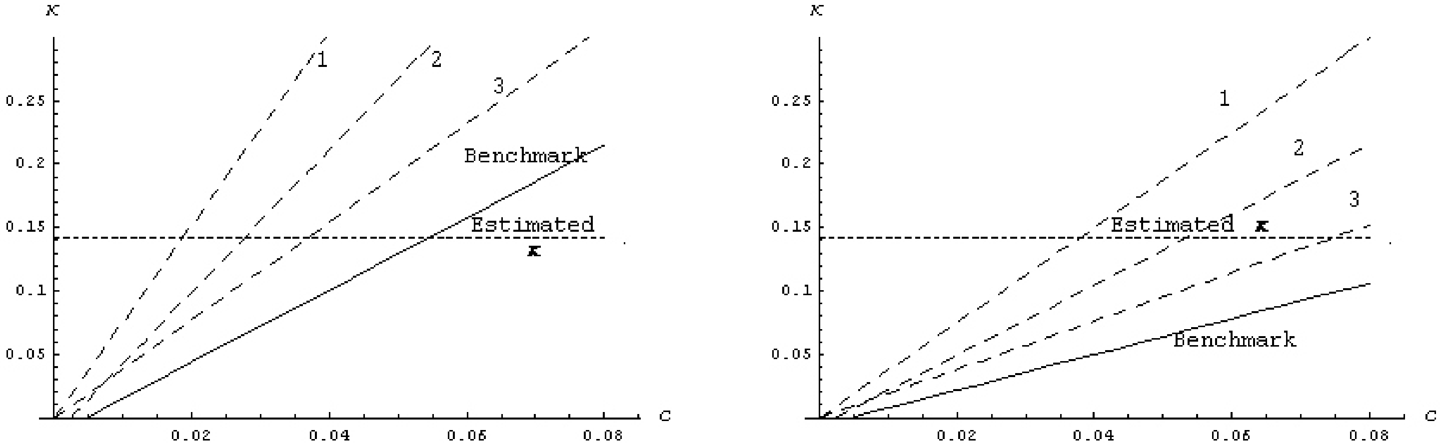


e) !Kung (F_{DG}=0.007)

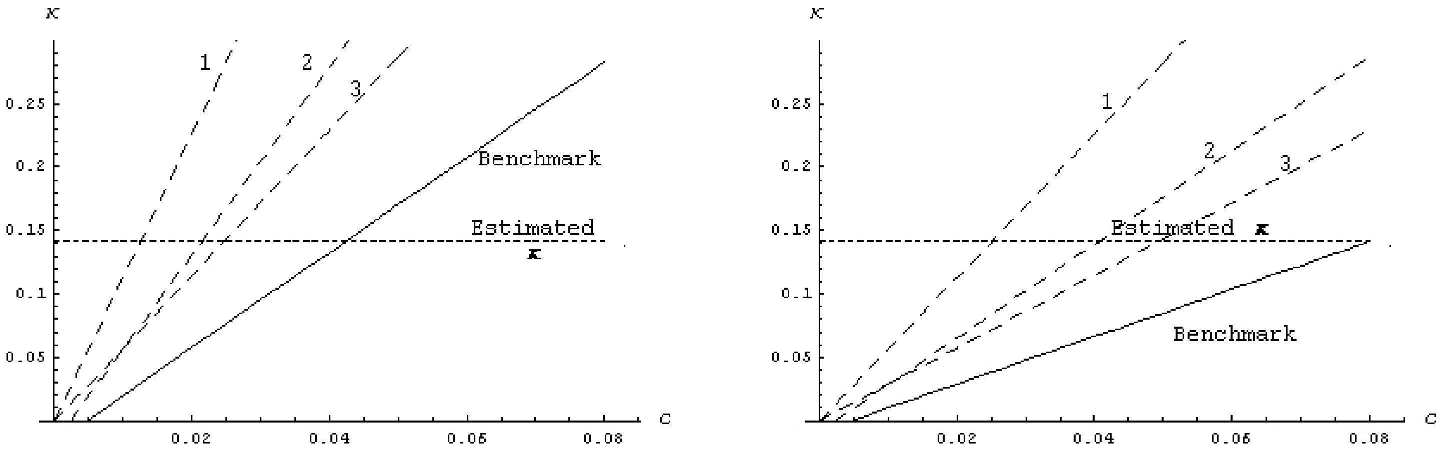




(f) SAfrican demes and Kaiadilt-Lardiil (Aus) (F_{DT}=0.081)



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	$r + (1\text{-}r)p$	$2p - r\text{-}(1\text{-}r)p$
N	$1\text{-}p$	$p - rp$	$2p - p + rp$

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 $d=(1-\cos\theta)^{1/2}(2(2^{1/2}))/\pi))$ (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	$\geq$5.0	Points embedded in bone only p183
Denmark (Vedbaek) (*61*)	4100BC	13.6	“affluent foragers”
Sweden (Sketeholm I) (*61*)	4300BC	$\geq$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

11. Works cited.

1. J. B. S. Haldane, *The Causes of Evolution* (Harper and Brothers, New York, 1932), pp.
2. S. Wright, *Genetics* **28**, 114 (1943).
3. I. Eshel, *Theoretical Population Biology* **3**, 258 (1972).
4. S. Boorman, P. R. Levitt, *Theoretical Population Biology* **4**, 85 (1973).
5. A. Traulsen, M. Nowak, *Proc. Natl. Acad. Sci. USA* **103**, 10952 (2006).
6. K. Aoki, *Evolution* **36**, 832 (1982).
7. A. R. Rogers, *American Naturalist* **135**, 398 (1990).
8. E. G. Neves, *Rev. do Museo de Arqueologica e Ethnologia (S. Paulo)* **5**, 195 (1995).
9. P. Smouse, V. Vitzthum, J. Neel, *Genetics* **98** (1981).
10. R. H. Ward, in *Methods and Theories of Anthropological Genetics* M. H. Crawford, P. L. Workman, Eds. (University of New Mexico Press, Albuquerque, 1973) pp. 367-388.
11. S. Wright, *Journal of Genetics* **30**, 257 (1935).
12. S. Bowles, H. Gintis, *Theoretical Population Biology* **65**, 17 (2004).
13. C. Boehm, *Hierachy in the Forest* (Harvard University Press, Cambridge, 2000), pp.
14. P. Wiessner, *Human Nature* (2005).
15. S. Wright, *American Naturalist* **56**, 330 (1922).
16. C. Keckler, in *Integrating Archaeological Demography: Multidisciplinary Approaches to Prehistoric Population* R. Paine, Ed. (Southern Illinois University, Center for Archaeological Investigations, 1997) pp. 205-228.
17. M. N. Cohen, in *Biosocial Mechanisms of Population Regulation* M. N. Cohen, Roy S. Malpass, and Harold G. Klein, Ed. (Yale University Press, New Haven, 1980) pp. 275-303.
18. J.-P. Bocquet-Appel, P.-Y. Demars, L. Noiret, D. Dobrowsky, *Journal of Archaeological Science* **32**, 1656 (2005).
19. J. B. Birdsell, *Cold Spring Harbor Symposium on Quantitative Biology* **22**, 47 (1957).
20. S. R. Johansson, S. R. Horowitz, *American Journal of Physical Anthropology* **71**, 233 (1986).

21. F. A. Hassan, in *Biosocial Mechanisms of Population Regulation* M. N. Cohen, Roy S. Malpass, and Harold G. Klein, Ed. (Yale University Press, New Haven, 1980).

22. B. Martrat, J. Grimalt, C. Lopez-Martinez, I. Cacho, F. Sierro, J. A. Flores *et al.*, *Science* **306**, 1762 (2004).

23. S. J. Johnsen, W. Dansgaard, J. W. C. White, *Tellus B41*, 452 (1992).

24. M. Mann, M. Bradley, M. Hughes, *Nature* **391**, 779 (1998).

25. J. McManus, D. Oppo, J. Cullen, *Science* **283**, 971 (1999).

26. C. Boehm, *Journal of Consciousness Studies* **7**, 211 (2000).

27. C. Ember, M. Ember, *Journal of Conflict Resolution* **32**, 242 (1992).

28. F. Wendorf, in *The Prehistory of Nubia* F. Wendorf, Ed. (Southern Methodist University Press, Dallas, 1968), vol. 2, pp. 954-998.

29. P. Lambert, in *Troubled Times: Violence and Warfare in the Past* D. L. Martin, D. W. Frayer, Eds. (Gordon and Breach, Ameterdam, 1997) pp. 77-109.

30. L. Keeley, *War Before Civilization* (Oxford University Press, New York, 1996), pp.

31. K. Hill, A. M. Hurtado, *Ache life history: the ecology and demography of a foraging people* (Aldine de Gruyter, 1996), pp.

32. R. C. Kelly, *Warless Societies and the Origin of War* (University of Michigan Press, Ann Arbor, 2000), pp.

33. J. Jorgensen, *Western Indians* (Freeman, San Francisco, 1980), pp.

34. C. R. Ember, M. Ember, in *Troubled Times: Violence and Warfare in the Past* D. L. Martin, D. W. Frayer, Eds. (Gordon and Breach Publishers, 1997).

35. R. C. Kelly, *The Nuer Conquest: The Structure and Development of an Expansionist System* (University of Michigan Press, Ann Arbor, 1985), pp.

36. M. Meggitt, *Blood is their argument* (Mayfield, Palo Alto, 1977), pp.

37. L. L. Cavalli-Sforza, W. F. Bodmer, *The Genetics of Human Populations* (W.H.Freeman, San Francisco, 1970), pp.

38. L. Binford, *Constructing Frames of Reference: An Analytical Method for Archeological Theory Using Hunter-Gatherer and Environmental Data Sets* (University of California Press, Berkeley, 2001), pp.

39. H. Kaplan, K. Hill, *Current Anthropology* **26**, 223 (1985).

40. M. Imhof, C. Schlotterer, *Proceedings of the National Acadamy of Science* **98**, 1113 (2001).

41. M. Lynch, J. Blanchard, D. Houle, T. Kibota, S. Schultz, L. Vassilieva *et al.*, *Evolution* **53**, 645 (1999).

42. E. Santiago, l. Ekunwe, N. Hajela, S. Oden, R. Lensky, *Genetica* **102-103**, 349 (1998).

43. D. Wloch, K. Szafraniec, R. Borts, R. Korona, *Genetics* **159**, 441 (2001).

44. J. Endler, *Natural Selection in the Wild* (Princeton University Press, Princeton, 1986), pp.

45. North Greenland Ice Core Project members, *Nature* **431**, 147 (2004).

46. Y. G. Rychkov, Sheremet'eva, in *The human biology of circumpolar populations* F. Milan, Ed. (Cambridge U Press, New York, 1980).

47. T. Karafet, L. Osipova, M. Gubina, O. Posukh, S. Zegura, M. Hammer, *Human Biology* **74**, 761 (2002).

48. H. C. Harpending, T. Jenkins, in *Genetic Distance* J. F. Crow, C. Denniston, Eds. (Plenum, New York, 1974).

49. H. C. Harpending, T. Jenkins, in *Methods and Theories of Anthropological Genetics* M. Crawford, P. C. Workman, Eds. (University of New Mexico Press, Albuquerque, 1973).

50. B. Keats, *Journal of Human Evolution* **6** (1977).

51. R. T. Simmons, N. B. Tindale, J. Birdsell, *Physical Anthropology* **20**, 303 (1962).

52. M. Tommaseo-Ponzetta, M. Attimonelli, M. De Robertis, F. Tanzariello, D. Saccone, *American Journal of Physical Anthropology* **117**, 49 (2002).

53. P. B. Roscoe, *Current Anthropology* **34**, 111 (1993).

54. L. Cavalli-Sforza, Ed., *African Pygmies* (Academic Press, Inc., New York, 1986), pp. 461.

55. L. L. Cavalli-Sforza, A. W. F. Edwards, *Evolution* **21**, 550 (1967).

56. L. L. Cavalli-Sforza, P. Menozzi, A. Piazza, *The History and Geography of Human Genes* (Princeton University Press, Princeton, 1994), pp.

57. J. Cybulski, in *In the wake of contact: Biological responses to conquest* C. S. Larsen, G. Milner, Eds. (Wiley-Liss, 1994) pp. 75-85.

58. S. Vencl, *L'Anthropologie* **95**, 219 (1991).

59. D. Telegin, *Arkheologiya* **XIII**, 3 (1961).

60. M. Moratto, *California Archaeology* (Academic, Orlando, 1984), pp.

61. T. D. Price, in *Prehistoric Hunter-Gatherers: The emergence of cultural complexity* T. D. Price, J. A. Brown, Eds. (Academic, Orlando, 1985) pp. 341-363.

62. K. F. Otterbein, *The Evolution of War: A Cross Cultural Study* (Human Relations Area Files, Inc., 1989), pp.

63. M. H. Ross, *Ethology* **22**, 169 (1983).

64. C. Ember, *Ethology* **17**, 439 (1978).