



The co-evolution of individual behaviors and social institutions

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Abstract

We present agent-based simulations of a model of a deme-structured population in which group differences in social institutions are culturally transmitted and individual behaviors are genetically transmitted. We use a standard extended fitness accounting framework to identify the parameter space for which this co-evolutionary process generates high levels of group-beneficial behaviors. We show that intergroup conflicts may explain the evolutionary success of both: (a) altruistic forms of human sociality towards unrelated members of one's group; and (b) group-level institutional structures such as food sharing which have emerged and diffused repeatedly in a wide variety of ecologies during the course of human history. Group-beneficial behaviors may evolve if (a) they inflict sufficient fitness costs on outgroup individuals and (b) group-level institutions limit the individual fitness costs of these behaviors and thereby attenuate within-group selection against these behaviors. Thus, the evolutionary success of individually costly but group-beneficial behaviors in the relevant environments during the first 90,000 years of anatomically modern human existence may have been a consequence of distinctive human capacities in social institution building.

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1. Introduction

Is the remarkable level of cooperation among unrelated humans a result of the distinctive capacities of humans to construct institutional environments which limit competition and reduce phenotypic variation within groups, allowing individually costly but group-beneficial behaviors to co-evolve with these supporting environments through a process of interdemic group selection? We use simulations of a standard extended fitness accounting framework to investigate this question, identifying the parameter space for which this co-evolutionary process generates high levels of group-beneficial behaviors.

The idea that the suppression of within-group competition may be a strong influence on evolutionary dynamics has been widely recognized in eusocial insects and other species (Smith and Szathmari, 1995; Frank,

1995; Michod, 1996; Buss, 1987; Ratnieks, 1988). Boehm (1982) and Irenaus Eibl-Eibesfeldt (1982) first applied this reasoning to human evolution, exploring the role of culturally transmitted practices which reduce phenotypic variation within groups. Examples of such variance-reducing practices are leveling institutions, such as monogamy and food sharing among non-kin, namely those which reduce within-group differences in reproductive fitness or material well-being. Monogamous or polygamous mating systems, distinct systems of resource sharing, and the like may be termed institutions, by which we mean a uniformity in the structure of human interactions, that is characteristic of a group but may differ among groups. Such structures may have attenuated within-group selection operating against individually costly but group-beneficial practices, resulting in higher group average fitness or material success. If so, groups adopting these variance-reducing institutions would have had advantages in coping with climatic adversity, intergroup conflicts and other threats. A group's institutions thus constitute a niche, that is, a modified environment capable of imparting distinctive

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direction and pace of evolutionary change (Laland et al., 2000; Bowles, 2000). According to this view, the evolutionary success of variance-reducing social institutions may be explained by the fact that they retard selection pressures working against in-group-beneficial individual traits coupled with the fact that high frequencies of bearers of these traits reduces the likelihood of group extinctions (or increases the likelihood of a group's expanding and propagating new groups).

The evolutionary mechanisms involved in this account are multi-level selection processes with the novel features (adapted from Bowles, 2001) that both genetically transmitted influences on individual behaviors as well as culturally transmitted group-level institutional characteristics are subject to selection, with inter-group conflicts playing a decisive role in group-level selection. The model is thus an example of a gene-culture evolutionary process (Cavalli-Sforza and Feldman, 1981; Boyd and Richerson, 1985; Durham, 1991).

It has been long recognized that in populations composed of groups characterized by a markedly higher level of interaction among members than with outsiders, evolutionary processes may be decomposed into between-group and within-group selection effects (Lewontin, 1965; Price, 1972; Crow and Kimura, 1970; Uyenoyama and Feldman, 1980). Where the rate of replication of a trait depends on the frequency of the trait in the group and where group differences in trait frequencies are substantial and persistent, group selection contributes to the pace and direction of evolutionary change. But most who have modeled evolutionary processes under the joint influence of group and individual selection have concluded that the group selection pressures cannot override individual-level selection except where special circumstances (e.g. small group size, limited migration) heighten and sustain differences between groups relative to within-group differences (Eshel, 1972; Boorman and Levitt, 1973; Smith, 1976).

Beginning with Darwin (for example Darwin, 1873; p. 156 and other passages), a number of evolutionary theorists have suggested that human evolution might provide an exception to this negative assessment of the force of multi-level selection. Haldane (1932) suggested that in a population of small endogamous “tribes”, an altruistic trait might evolve because the “tribe splitting” which occurs when successful groups reach a certain size would create a few successor groups with a very high frequency of altruists, reducing within-group variance and increasing between-group variance, a process very similar to that simulated in this paper (pp.210ff). Hamilton (1975) took up Haldane's suggestion, adding that if the allocation of members to successor groups following tribe splitting was not random but was rather

what he called “associative” (p.137), group selection pressures would be further enhanced. Subsequently, a number of writers have pointed out that group selection may be of considerably greater importance among humans than among other animals given the advanced level of human cognitive and linguistic capabilities, the consequent capacity to maintain group boundaries and to formulate general rules of behavior for large groups, and the resulting substantial influence of cultural inheritance on human behavior (Alexander, 1987; Cavalli-Sforza and Feldman, 1973; Boyd and Richerson, 1985, 1990; Sober and Wilson, 1994; Boehm, 1997; Gintis, 2000).

It is now widely accepted that the distribution of culturally transmitted traits (i.e. learned behaviors) may be strongly influenced by group selection pressures (Boyd and Richerson, 2002; Soltis et al., 1995). But many doubt the importance of group selection for traits governed by genetic transmission. Whether they are right is an empirical question: could a genetically transmitted altruistic trait evolve under the influence of group selection pressures in an environment approximating past human social and ecological interactions? This is the question our simulations seek to answer.

Among the distinctive human characteristics which may enhance group selection effects on genetic variation is our capacity for the suppression of within-group phenotypic differences in reproductive or material success, our patterns of social differentiation supporting positive assortment (non-random pairing), and the frequency of intergroup conflict. Thus, the two key features of our model will be intergroup conflicts and culturally transmitted group differences in institutional structure. We stress intergroup conflicts for empirical reasons: the central role of war and the extinction or reduced fitness of loser populations in the spread of behavioral traits. The institutions we model are the commonly observed human practices of resource sharing among group members including non-kin and patterns of residence and social differentiation that result in a greater likelihood of like types interacting (positive assortment). Our model could easily be extended to study other group level institutions that, like resource sharing, reduce the within group variance of material and hence reproductive success. Included are information sharing, consensus decision making, and monogamy.

Group differences in institutional structure persist over long periods of time due to the nature of institutions as conventions. A convention is a common practice that is adhered to by virtually all group members because the relevant behaviors—for example sharing meat, or not engaging in extra-pair copulations—are mutual best responses conditional on the expectation of similar behaviors by most others (Young, 1995). We do not here model the reasons why the

behavior prescribed by the institution is a mutual best response, but plausible accounts are not difficult to provide. Those violating sharing norms may bear fitness costs of ostracism, for example (Boehm, 1993). The conventional nature of institutions accounts for their long-term persistence and also their occasional rapid demise under the influence of shocks. We study institutional evolution in ways analogous to the evolution of individual traits. Just as the individuals in our model are the bearers of genes, groups are the bearers of institutions, and a successful institution produces many replicas, while unsuccessful ones are eliminated. The inheritance of group-level institutions results from a cultural transmission process based on learned behaviors: as new members of the population mature or immigrate, they adhere to the existing institutions, not due to any conformist predisposition, but because this is a best response as long as most others do the same. The resulting behavioral uniformity in adherence to a group's institutions permits us to treat the institution as a group-level characteristic.

By contrast, the group beneficial individual traits in our model are replicated by a standard fitness-based mechanism in which the above pressures for uniformity are absent. We consider a single individually costly but group-beneficial trait relevant to dyadic interactions among group members. Other formally altruistic traits could be modeled in a similar manner. Included are individual contributions in an n -person public good interaction (common defense, insurance as modeled in Bowles and Gintis, 2003), or the punishment of those who fail to contribute in such situations, and other ways that cheating is sanctioned (e.g. Clutton-Brock and Parker, 1995; Boyd et al., 2003). Our simulations seek to determine the environments in which such a trait, if initially rare, can proliferate in the population.

2. Social institutions and multi-level selection

The causal importance of social institutions in our simulations will be illuminated by a simple model of multi-level selection in which between-group conflicts are absent. (We introduce these presently). Consider a single trait, which may be absent or present in each individual in a large population, the members of which each belong to one of a number of groups. For concreteness, consider an altruistic behavior which costs the individual c and confers a benefit of b (both measured in units of some material resource) on a randomly paired (single) other member of the group. To simplify this example, suppose that differences in material payoffs are expressed directly as differences in fitness. This means that a member in a group composed entirely of A's (that is, altruists) has material payoffs exceeding those of a member in another group with no

altruists by the amount $b-c$, with fitness correspondingly higher as well. As we assume $b-c > 0$, altruism is group-beneficial. But in any mixed group, the expected payoffs and fitness of altruists will be lower than that of the N's (the non-altruists).¹ So within-group selection will work against the altruists.

**The Altruism Game:
Row's Payoffs**

	A	N
A	$b-c$	$-c$
N	b	0

Let $p_{ij} = 1$ indicate that individual i in group j has the trait, with $p_{ij} = 0$ otherwise (those without the trait are N's). Using a discrete time framework, let p and p' represent the fraction of the population with the trait during a given time period and the subsequent period, respectively, and $\Delta p \equiv p' - p$.² Price (1972) showed that Δp can be partitioned into group and individual effects. Define w_{ij} as the number of offspring, next period, of an individual of type i in group j . Let w_{ij} depend additively on type i 's own trait and on the frequency of the trait in the group ($p_j \in [0, 1]$) according to:

$$w_{ij} = \beta_0 + p_j \beta_g + p_{ij} \beta_i, \quad (1)$$

where β_g and β_i are the partial effects on w_{ij} of the frequency of the trait in the group and the presence of the trait in the individual, respectively (the subscripts refer to group and individual effects) and β_0 , a constant, captures other influences on fitness. Define $\beta_G \equiv \beta_g + \beta_i$ as the effect on the group average number of replicas of the frequency of the trait in the group (the difference in the number of offspring of an individual in a group composed entirely of those with the trait and a group entirely without is β_G). Thus using the definitions above, $\beta_i = -c$, $\beta_g = b$ and $\beta_G = b - c$. Then following Price (1972), and taking the expected value of Δp as an

¹ For groups of infinite size the expected difference in payoffs is c . As Pepper (2000) shows, the "large group" assumption is required for this approximation because in a q -person group with $q_A < q$ A's, the probability that an A will be paired with another A under random pairing is not $p_j \equiv q_A/q$, but $(q_A - 1)/(q - 1) < p_j$. The discrepancy arises because the individual A-member cannot be paired with itself. As a result, for finite group size, the difference in average payoffs of the A's and the N's is not c but rather $c + b/(q - 1)$. For large populations the discrepancy may be ignored, as it is in order to simplify the presentation in this section. In the simulations below, the "large group" assumption is dropped and the relevant probabilities reflect the actual group size.

² We thus do not provide an explicit treatment of the mating system and genotype-phenotype relationship but instead assume that the behavior in question is the expression of a single gene, and that reproduction is asexual.

adequate approximation of Δp due to the large population size assumed, we have

$$w\Delta p = \text{var}(p_j)\beta_G + E\{\text{var}(p_{ij})\}\beta_i \tag{2}$$

or

$$w\Delta p = \text{var}(p_j)(b - c) - E\{\text{var}(p_{ij})\}c,$$

where w is the population-wide average of the number of offspring (which we normalize to unity) and the expectation operator $E\{\}$ indicates a weighted average over groups (the weights being relative group size). The first term captures the group-selection effect (which is positive), while the second represents the effect of individual selection, which is negative (a simple derivation of this decomposition is in Bowles (2001)). Setting aside degenerate cases such as zero variances, it follows that an interior frequency of the trait will be stationary where these two terms are of equal absolute magnitude (assuming that the β 's and variances making up these terms are themselves stationary). Because the second term is negative, the frequency of the A-trait within all surviving groups will fall over time. But as β_G is positive, this tendency will be offset by the continual extinction of groups with disproportionately low frequencies of the trait and their replacement by “new” groups with disproportionately high frequencies.

Then rearranging the stationarity condition for p (2) we see that $\Delta p = 0$ when

$$c/b = \text{var}(p_j)/[E\{\text{var}(p_{ij})\} + \text{var}(p_j)] \tag{3}$$

with

$$\Delta p > 0 \text{ for } c/b < \text{var}(p_j)/[E\{\text{var}(p_{ij})\} + \text{var}(p_j)]$$

$$\Delta p < 0 \text{ for } c/b > \text{var}(p_j)/[E\{\text{var}(p_{ij})\} + \text{var}(p_j)].$$

The left-hand term is the benefit-to-cost ratio of the altruistic trait. The right-hand term is the ratio of between-group to the within-group plus the between-group variance of the trait. It is easily shown (Crow and Kimura, 1970) that this ratio measures the difference between the probabilities that an altruist will be paired with an altruist, $P(A|A)$, and that a non-altruist be paired with an altruist, $P(A|N)$. Thus

$$r \equiv \text{var}(p_j)/[E\{\text{var}(p_{ij})\} + \text{var}(p_j)] = P(A|A) - P(A|N).$$

The variance ratio, r , is thus a population-wide measure of the degree of non-randomness resulting not because of non-random pairing within groups, but because the population is group-structured. Eq. (3) shows that in order for an altruistic trait to proliferate in a population, the more costly (relative to the benefits) is the trait, the greater must be the between-group variance (relative to the within-group variance).

When the variance among group means is zero, A's no longer have the advantage of being in groups with disproportionately many A's. In this case group selection is inoperative, so only a costly form of group benefit

could proliferate. By contrast when $\text{var}(p_{ij}) = 0 \forall j$, groups are either all A or all N, and one meets only one's own type, independently of the composition of the total population. In this case, within-group selection is absent and between-group selection is the only selective force at work.

Thus the force of group selection will depend on the magnitude of the group benefit relative to the individual cost (b and c in the example) and the degree to which groups differ in their frequency of the trait, relative to the degree of within-group variance of the trait. Rewriting Eq. (3) as $rb - c = 0$ we see that the stationarity condition for p in a group-structured population is just another version of Hamilton's rule for the degree of positive assortment permitting an altruistic trait to proliferate when rare. In this respect, multi-level selection works by the same processes as other evolutionary processes based on non-random pairing.

Fig. 1 shows how the group structure of the population overcomes the disadvantage of bearing the costs of altruistic behaviors. While the expected payoff to the non-altruist (π_N) exceeds that to an altruist (π_A) when they both have the same probability of being paired with an altruist, the difference in the probability of meeting an altruist conditional on one's type may overcome this disadvantage. The figure illustrates a value of the variance ratio r (that is, the difference $P(A|A) - P(A|N)$) that is just sufficient to equate the expected payoffs of the two types and thus to maintain a stationary value of p . How large this difference must be depends, as we have seen and as the figure makes clear, on the payoff differences between the bearers of the two traits.

Group level social institutions may reduce these within group payoff (and hence fitness) differences between the A's and the N's. To explore these effects

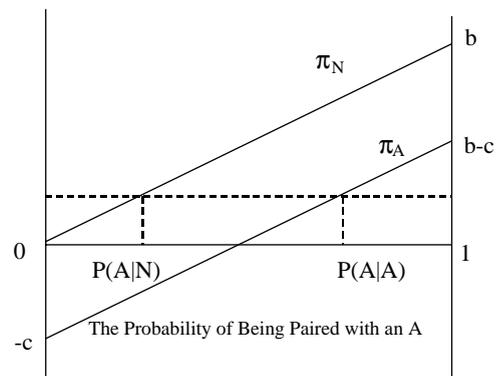


Fig. 1. The evolution of an altruistic trait in a group-structured population. If the population structure's variance ratio is such that the difference in the conditional probabilities of being paired with an A ($P(A|A) - P(A|N)$) is as shown ($r = r^*$), p is stationary, because the expected payoffs of the two types π_A and π_N are equal.

of institutions we need to model the process of differential replication. Suppose that in the absence of the group-level institutions (to be introduced presently) the selection process within a group is modeled (for group j) by the standard replicator dynamic equation

$$\Delta p_j = p_j(1 - p_j)(\pi^A - \pi^N) = p_j(1 - p_j)(-c). \quad (4)$$

Now imagine that the group has adopted the practice, common among foragers and other human groups, of within-group resource sharing. Some fraction of the resources an individual acquires—perhaps specific kinds of food as among the Ache (Kaplan and Hill, 1985)—is deposited in a common pot to be shared equally among all group members. This sharing institution may be modeled as a linear tax, $t \in [0, 1)$, collected from the members payoffs with the proceeds distributed equally to all members of the population. The effect is to reduce payoff differences between A's and N's, that is: $\pi^A - \pi^N = -(1 - t)c$. Fig. 2 shows the effect of resource sharing on the payoff differences of the two types. The difference in the probability of meeting an A (conditional on ones own type) that equalizes expected payoffs is no longer $P(A|A) - P(A|N) = r^*$ as shown in Fig. 1, but is now $P^T(A|A) - P^T(A|N) = r^T$ with $r^T < r^*$. Comparing the two figures one sees that $r^* = c/b$ while $r^T = c(1 - t)/b$. As a result, were the population structure as in Fig. 1 (r^*) and the sharing institution in place ($t > 0$), then $\pi_A > \pi_N$, so p would increase.

Suppose that in addition to the institution of resource sharing, groups are also segmented, so that in the pairing process within groups, A's are more likely to interact with A's and N's with N's than would occur by random matching. Suppose that the probability that an A-member of group j is matched with an A is not p_j but $s_j + (1 - s_j)p_j \geq p_j$ and the probability that a N-member of group j is matched with an A is $(1 - s_j)p_j \leq p_j$. Then we define $s_j \geq 0$ as the degree of segmentation in group, or the difference in the conditional probability of an A

meeting an A and an N meeting an A in the within-group pairing. A transparent interpretation of s_j is that it represents the fraction of interactions that take place with one's own type for reasons such as common residence and the like, the remaining $(1 - s_j)$ pairings being random. But it could arise for other reasons, deliberate but imperfect attempts by the A's to avoid interactions with the N's, for example. Then ignoring the subscripts, and abstracting from the tax: $\pi^A - \pi^N = sb - c$. Segmentation reduces the expected payoff disadvantage of altruists because within a given group they are disproportionately likely to meet other altruists, while N's are disproportionately likely to meet other N's. If $s > c/b$, A's will on average do better than N's within every group and as a result the A's will proliferate as a result of both within and between-group selection. Thus, both terms in the Price equation will be positive. To pose the classical group-selection problem, we assume $s < c/b$, so the A's will only proliferate if group-selection pressures are strong enough. Like resource sharing, segmentation is a convention and is passed on culturally.

Taking account of both segmentation and resource sharing, the differences in the expected payoffs received by N's and A's within a group will now be $(1 - t_j)(s_j b - c)$ so we have

$$\Delta p_j = p_j(1 - p_j)(1 - t)(sb - c) \quad (5)$$

from which it is clear (comparing (5) and (4)) that both institutions retard the within-group selection against the A's. This can be seen by noting that

$$\begin{aligned} \partial \Delta p_j / \partial t &= -p_j(1 - p_j)(sb - c), \\ \partial \Delta p_j / \partial s &= p_j(1 - p_j)(1 - t)b. \end{aligned} \quad (6)$$

For $p_j \in (0, 1)$ both expressions are positive, meaning that both segmentation and resource sharing attenuate the negative selection against the A's. Note that the effect of each institution is greater when p_j is close to one half, and when the other institution is at a low level. Thus, in terms of their benefits in retarding selection against the A's, for a given level of p_j , the institutions are substitutes, not complements: their beneficial effects are enhanced the lesser is the presence of the other.

The model shows how group level institutions may retard individual level selection and thus facilitate the proliferation of an otherwise unviable trait by means of group selection. But the analysis is incomplete. The Price equation gives the stationarity condition for p , but it does not account for the movement of the variances upon which the movement in p is based. For most species, the between-group variance-enhancing mechanisms (mutation, genetic drift) are weak and tend to be swamped by the homogenizing effects of selection itself, along with migration among groups. This is the reason why group-selection pressures among non-human

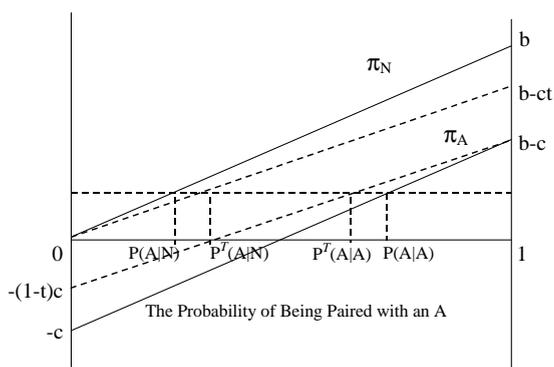


Fig. 2. Resource sharing increases the relative importance of population structure in the evolution of an altruistic trait. The dashed payoff functions indicate the effect of within group resource sharing; the altruistic trait will proliferate if $r = r^*$.

animals are thought to be weak. However, among humans, where effective group size is small (e.g. the members of a foraging band) and where groups frequently divide either in response to increased size or to interpersonal tensions within the group, a process of even random (rather than Hamilton's "associative") division will increase between-group variance.

Thus small group size and frequent group division coupled with social institutions that attenuate the within-group selection against the A-trait constitute an environment favorable for multi-level selection pressures to support the evolution of the A-trait. For any model even minimally faithful to the empirical circumstances of human evolution, the only practical way to determine if these between group variance-enhancing effects and within group attenuation of individual level selection are strong enough to make group selection an important influence on evolution is to simulate a group-structured population under reasonable parameter values.

3. An agent-based model of multi-level selection

We simulated an artificial population living in 20 groups. For each simulation, total population size is given and group size is approximately constant, modified only by random migration among groups and by the outcomes of group conflict, as explained below. In the model above, groups with a high frequency of A's produce more offspring and thus grow in size. In the simulations to follow, a group's size is restricted by its site, and a high frequency of A's contributes to the group's success in intergroup conflicts, allowing it to occupy a new site and thus to increase in size.

Reflecting the effect of payoffs on fitness, an individual's expected share of the group's next generation's offspring is equal to the individual's share of the group's total payoffs. We assume that each individual has access to material resources from sources other than the interaction we are modeling and set these "baseline payoffs" at 10 units. Because offspring are produced in proportion to the individual's share of the group's total material payoffs and the expected difference in payoffs is approximately $c = 1$ (in the absence of segmentation and resource sharing), the N's produce 10% more offspring than the A's. Individual replication is subject to mutations, such that with a small probability, e , the offspring of an A will be an N or an A with equal probability and conversely.

The institutions represented by s and t differ among groups, and they also evolve. When conflict occurs between groups, the group with the higher total payoff wins. The losing group's members die and the winning group populates the site occupied by the losers with

Table 1
Key parameters for the simulations

	Benchmark values	Range explored
Mean group size (n/g)	20	7–47
Migration rate (m)	0.2	0.1–0.3
Probability of conflict (k)	0.25	0.18–0.4
Mutation rate (e)	0.001	0.01–0.000001

Note: Total population size is n , and there are g groups; m , k and e are per generation. Other Parameters: benefit (b): 2; cost (c): 1; baseline payoffs: 10. We varied group size by varying n . For reasons explained in the text, we restricted s to not exceed 1/2 while $t \in [0, 1]$. The costs imposed on the group by these institutions are $(s^2 + t^2)/2$.

replicas of themselves.³ The new inhabitants of the site adopt the institutions of the group from which they descended. Institutions are also subject to stochastic variation, increasing or lowering t and s by chance each period. Both segmentation and resource sharing impose costs on the groups adopting them. More segmented groups may fail to capture the benefits of diversity or of economies of scale, and resource sharing may reduce incentives to acquire the resources to be shared. Neither of these costs are modeled formally, but to capture their impact, group average benefits are reduced by an amount that is rising and convex in both s and t . Unlike many institutions, both s and t may be introduced at low levels, so the initial emergence of resource sharing and segmentation could readily take place through the extension to an initially small number of unrelated individuals of the practice of within-family resource sharing or a preference for interaction with individuals sharing common traits, proximity, or other similarities.

The benchmark values of the parameters in the simulations, and the range of alternative values that we explored appear in Table 1. The structure of our simulation is described in Fig. 3 and its notes. (Additional details are available at http://www.santafe.edu/~bowles/artificial_history).

The key parameters concern the rate of (random) migration among groups, group size, and the probability in any period that a group will engage in a between-group conflicts. Because our group conflicts are lethal for the losers, we have chosen a benchmark probability of conflict giving an expected frequency of a single war every four generations. Of course group conflicts more commonly result in fitness differentials between winners and losers without group extinctions. Our benchmark likelihood of an extinction is chosen to reflect the long term consequences of plausible values of differential reproductive success between adjacent stronger and

³ An alternative formulation would have the losing group survive as a subordinated people with less access to resources and hence reduced fitness. We have modeled group conflict in this way elsewhere (Bowles and Choi, 2003a) but will not pursue it here.

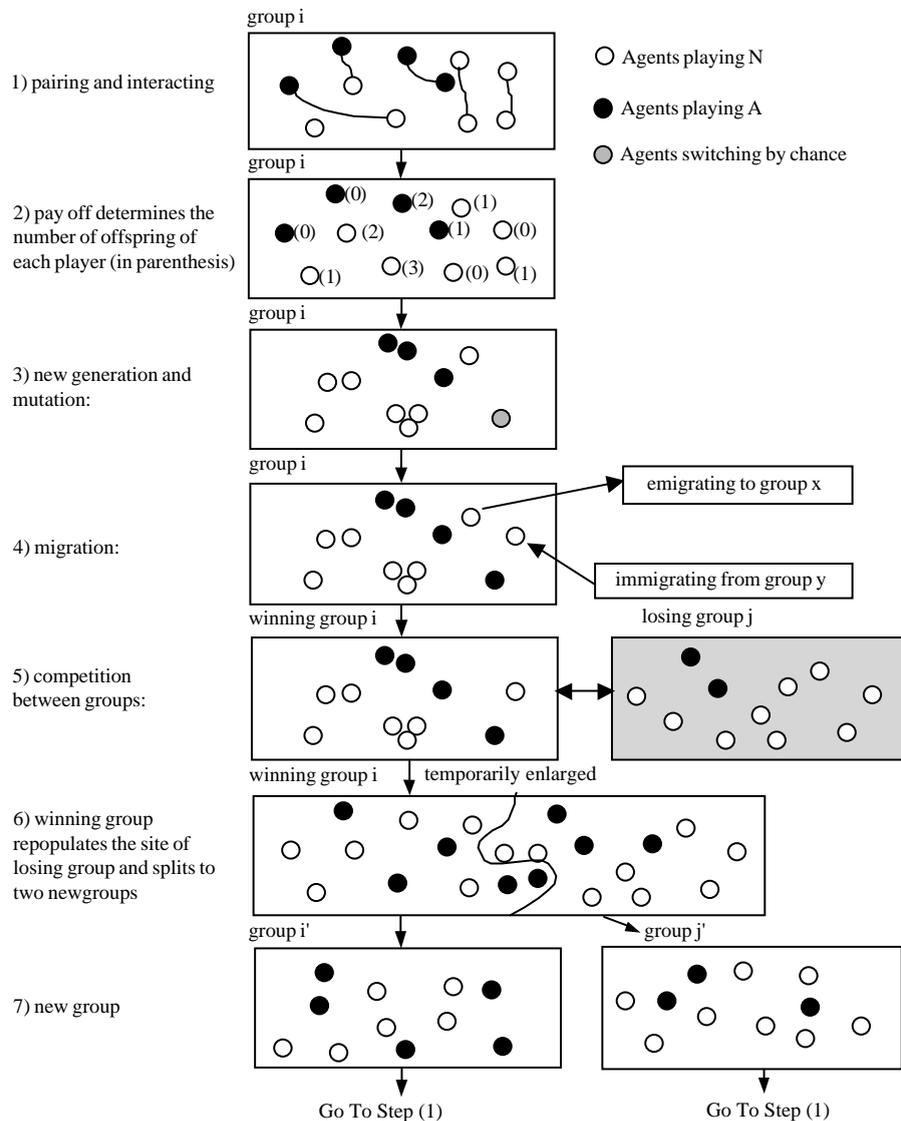


Fig. 3. Individual and group-level selection in the simulation. *Notes.* We assign n individuals to g groups. At $t=0$ all are N. 1. *Pairing.* In each period, each member of a group is randomly paired to play the PD game once, with another member with payoffs given in the text (in some runs modified by the resource-sharing rule). With segmentation, the member interacts with a similar type with probability s and is paired randomly with probability $1-s$. 2. *Reproduction.* Replicas of the current generation constitute the next generation. They are produced by drawing (with replacement) from the current group membership with the probability that any member will be drawn equal to that member's share of the total payoffs of the group. 3. *Mutation.* With probability e a member of the next generation is not a replica of its parent, but is A or N with equal probability. 4. *Migration.* With probability m each member of the new generation relocates to a group randomly selected from the other groups. 5. *Group competition.* With probability k each group is selected and among those selected competition takes place between randomly paired groups. The winning group is that with the highest total payoff (net of the costs of sharing and segmentation, if any). 6. *Repopulation and fission.* The members of the losing group are replaced by replicas of the members of the winning group, and the resulting (temporarily enlarged) winning group splits with members assigned randomly to two new groups. (In simulations with resource sharing or segmentation, the two new groups adopt the institutions of the winning group.)

weaker groups engaged in on going conflict. The other benchmark values were also chosen on grounds of empirical plausibility, the evidence for which we review in the penultimate section.

We initiated each simulation with altruists and institutions absent at time zero, to see if both the individual A-trait and the group level institutions would proliferate if initially rare (the individual and institu-

tional mutation process will introduce some variability in the population). To explore the effects of varying parameter values, we ran at least 10 simulations of at least 10,000 generations for each parameter set investigated, as indicated in the notes to Fig. 6.

The early generations of a typical simulation appear in Fig. 4. The rise in p is supported by the chance increase in both s and t (between periods 100 and 150).

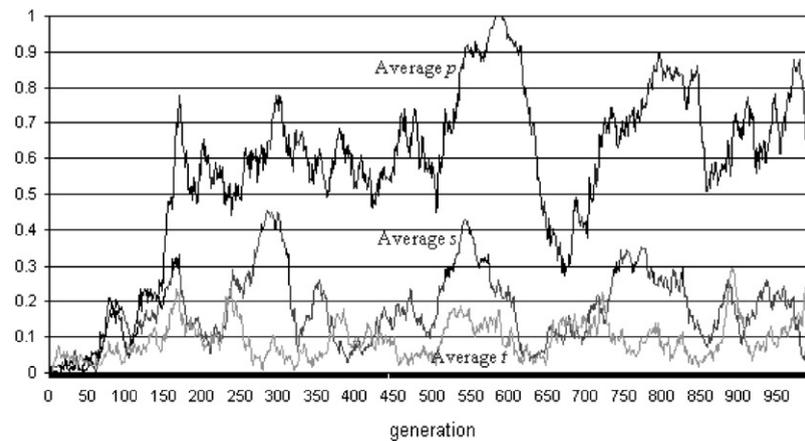


Fig. 4. The dynamic interaction between group institutions and individual behaviors. The figure presents a 1000 period history of a run using the benchmark parameters from Table 1. The population average frequency of altruists is p , while t and s give the average across the 20 groups of the level of resource sharing and segmentation. Altruism and both group-level institutions are initially rare. The particular time frame shown in Fig. 4 was selected because it clearly reveals this dynamic, which is observed over long periods in many runs.

When p reaches high levels (periods 532–588, for example) both s and t decline, typically leading to a sharp decline in p . The subsequent rise in s or t occurs by chance. This pattern emerges for the following reason. When the population is evenly divided between A's and N's, many groups are also approximately evenly divided. From Eq. (6), we know that the beneficial effects of institutions—the retarded within-group selection gained by higher levels of t or s —are maximized in this region. When p is well above 0.5, the benefits of the protection of A's offered by the institutions is of less value. But the institutions are costly to bear, so when p is high, groups with substantial levels of segmentation or resource sharing are likely to lose conflicts with other groups, and the sites they occupied are then populated by the descendants of winners, who typically bear lower levels of these institutional variables. As a result, both s and t fall.

To explore further the impact of institutions on the updating process we estimated the Price equation statistically, exploring the effect of institutions (that is, constraining s , t , both, or neither to zero). Using data from four simulations of 10,000 generation each, we regressed the observed Δp on the previous period's values for $\text{var}(p_j)$ and $E\{\text{var}(p_{ij})\}$, where the second term is the mean across all groups of the within-group variances. The coefficients of these variables are estimates of β_G and β_i from Eq. (2), respectively. As Table 2 shows, the combined effect of resource sharing and segmentation is to reduce by half the extent of within-group selection against the altruists, that is, the estimate of β_i is -0.102 without institutions and -0.055 with both institutions. Note that with no institutions the estimate of β_i (0.102) is very close to the expected value given that the baseline fitness is 10 (so N's have a 10% advantage in fitness). The estimate of the between-group

Table 2

Institutions retard within-group selection against altruists

Institutions	β_i	$-t$
None	-0.102	8.5
Resource sharing	-0.080	16.6
Segmentation	-0.063	4
Both	-0.055	11.2

Note: Column β_i gives the ordinary least-squares estimate of the coefficient of the group mean value of $p_j(1-p_j)$ as a predictor of Δp_j (the other regressor is the between-group variance, i.e. $\text{var}(p_j)$). The last column is the negative of the t -statistic for the estimate.

Table 3

An estimate of the price equation

Institutions	Effects ratio	Variance ratio	p
None	0.252	0.134	0.063
Both	0.127	0.132	0.516

Note: The second column is the ratio $-\beta_i/\beta_G$, estimated as described in Table 2, while the third column is the mean of $\text{var}(p_j)/E\{\text{var}(p_{ij})\}$ over the same simulations; p is the average fraction of A's in the population for these runs.

effect, β_G , varies little in response to which institutions are allowed to evolve, and is in all cases more than four times as large as the within-group effect. The mean within-group variance is correspondingly much larger than the between-group variance.

Note that we can rewrite Eq. (2), the condition for $\Delta p = 0$, as

$$-\beta_i/\beta_G = \text{var}(p_j)/E\{\text{var}(p_{ij})\} = R \quad (2')$$

with $\Delta p > 0$ if the variance ratio, R , exceeds the ratio of within- to between-group effects, and conversely. Do we observe this in our simulations? Using the econometric estimates of the within and between-group effects described in Table 2 as well as the mean variance ratios

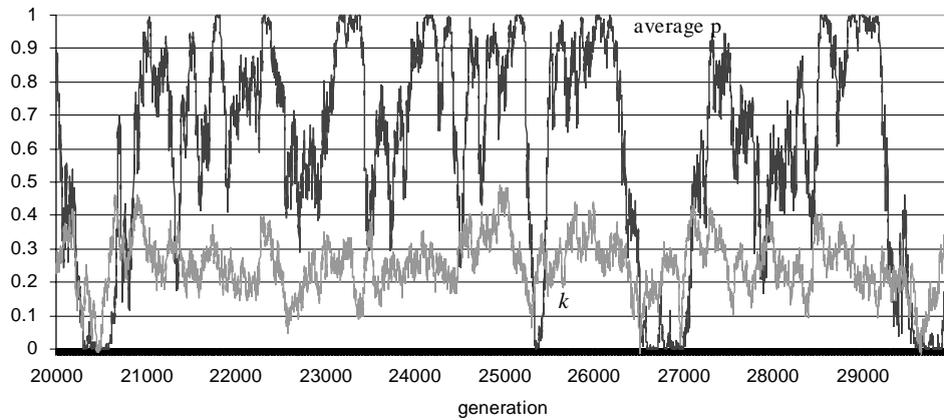


Fig. 5. High frequencies of group conflict favor altruism. The figure shows a thousand generation period from a run in which both institutions evolved endogenously, and in which k , the frequency of between-group conflict varies over time according to $k_t = k_0 + \rho k_{t-1} + \sigma_t$ where $\rho = 0.99$, σ_t is randomly drawn from the uniform distribution $[-0.02, 0.02]$, and k_0 is selected so that the mean of k_t is the same as the baseline k , namely, 0.25.

observed in the same simulations, we have the results in Table 3. With both institutions constrained to zero, the ratio of the within-group selection effect to the between-group selection effect, $-\beta_i/\beta_G$, is almost twice the ratio of between to within-group variances. Thus, were the population at these mean and estimated values, Δp would be negative. Thus it is no surprise to find that in the simulations on which these estimates are based, the mean value of p is 0.06. However, with both institutions unconstrained, the variance ratio is approximately equal to the effects ratio, meaning that the within-group effects operating against the A's are exactly offset by the between-group effects supporting their proliferation. In the simulation on which these estimates are based the mean value of p is 0.516.

Between-group conflicts play a key role in supporting both group-level institutions and individual-level altruism. In the simulations reported, the expected frequency of conflict was $1/k$, where k is the probability that a group is drawn for a conflict in every generation. It seems likely that over long historical periods, the frequency of conflict varied considerably, perhaps in response to the need to migrate in times of climatic variability. To explore the sensitivity of the simulations to the frequency of conflicts, we varied k stochastically using the auto-regressive system described in the notes to Fig. 5. During periods in which conflict was frequent (e.g. around the 21,000th generation), high levels of altruism were sustained, but periodic outbreaks of relative peace among the groups (around the 25,300th, 27,000th and 29,600th generations) led to sharp reductions in the fraction of A's in the population. The 500-generation period following generation 28,500 illustrates the strong path dependency in the model. The high level of p induced by the sharp rise in the frequency of intergroup conflict around 28,500 persists even as the frequency of conflict sharply declines in subsequent

generations. But the “lock-in” is not permanent: when k remains below 0.2 for a number of periods, p crashes.

We sought to answer two other questions as well. Could altruism have evolved had group level institutions not co-evolved with individual level altruism? And how sensitive are our simulations to variations in the key parameters? To answer these two questions, we varied group size from 7 to 47, and for each size ran 10 simulations of 50,000 generations, with the other parameters at their baseline values. We did this with both institutions constrained to not evolve, with each singly constrained to not evolve, and with neither constrained. We performed the same operation for variations in the migration rate from 0.1 to 0.3, and the probability of conflict (k) from 0.18 to 0.51. The results appear in Fig. 6.⁴

The top panel shows that with both institutions constrained not to evolve, a group size of 7 supports high levels of altruism, but group sizes greater than 8 result in a frequency of altruists of less than 0.3. Taking as a benchmark the group size for which $p > 0.5$, we see that with no institutions, the critical size is 8, while with both institutions, $p > 0.5$ for all group sizes less than 22. The results for the migration rate are similar. Without institutions, sustaining $p > 0.5$ requires a (per generation) migration rate of 0.13, but with both institutions free to evolve, the critical migration rate is 0.21. The bottom panel shows that institutions also allow the evolution of substantial frequencies of altruism with significantly fewer between-group conflicts. A “vertical” reading of the figure is also illuminating: for example,

⁴We also investigated whether the institutions would evolve if p is constrained to zero. They do not, because institutions are costly and where there are no altruists in the population they perform no group-beneficial function, thus leading groups that by chance adopt a high level of sharing or segmentation to lose conflicts in which they are involved.

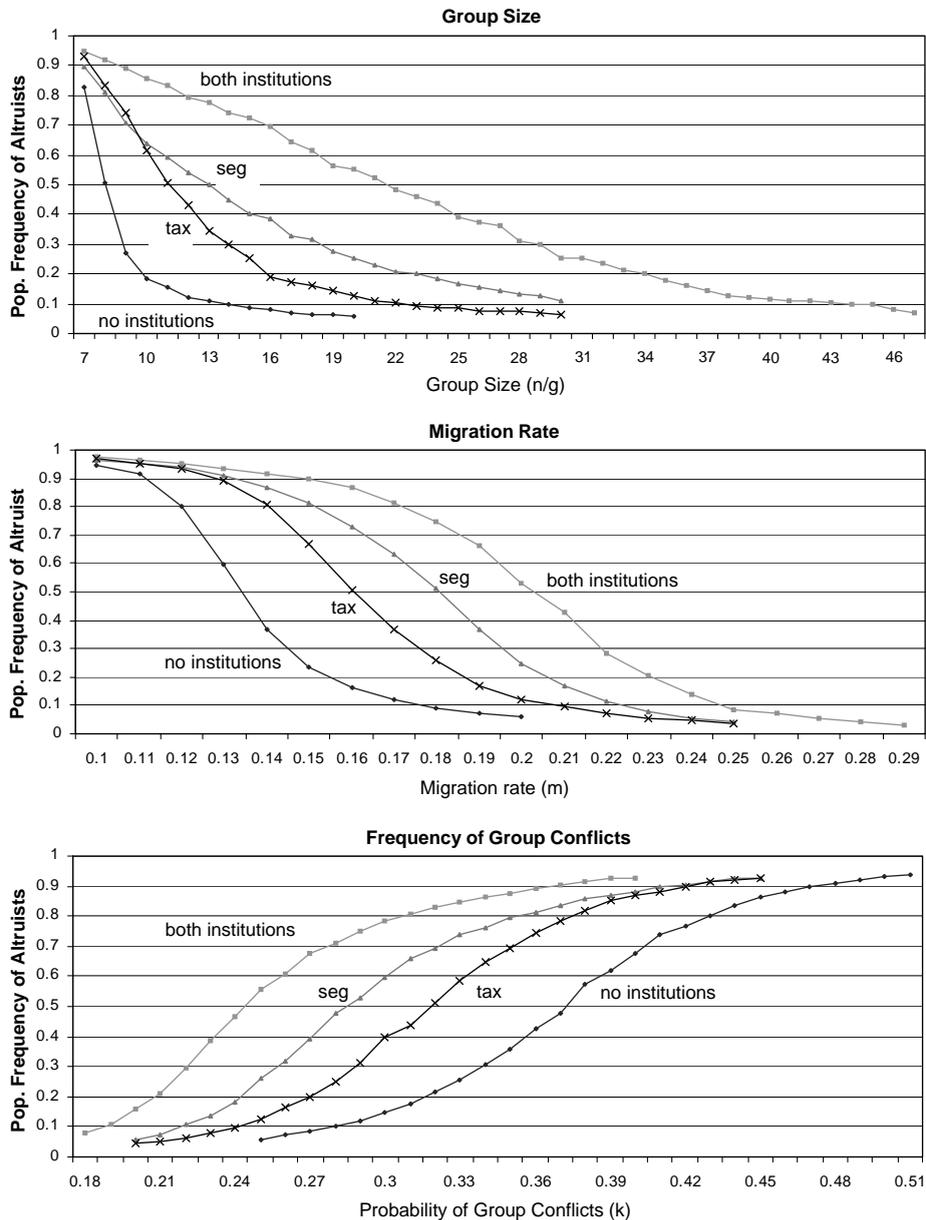


Fig. 6. Group-level institutions increase the size of the parameter space for which altruistic behaviors are common. *Notes.* Each data point is the average frequency of altruists in the entire population over 10 runs of 50,000 periods each for the parameter value indicated on the horizontal axis. In each panel the other parameters are the benchmark values shown in Table 1. Each run began with p , t , and s set equal to zero. The curve labeled “none” gives the results for runs in which t and s were constrained to zero; the other curves indicate runs in which one or both of the institutions were free to evolve. (“Tax” refers to resource sharing.) The horizontal distance between the curves indicates the enlargement of the parameter space made possible by group level institutions. The vertical distance between the curves shows the impact of institutions on average p .

the bottom panel shows that for $k = 0.3$, p is less than 0.2 without institutions, but is greater than 0.8 with both institutions free to evolve.⁵

⁵ Fig. 6 and Table 2 suggest that segregation is a more powerful influence than resource sharing: the segmentation alone has a larger effect than resource sharing alone both in retarding within-group selection against the A’s and in broadening the parameter space for which the A’s constitute large fractions of the population. This is artifact of our modeling choices. The cost functions for s and t are identical but s has a greater impact on within-group updating, as can be seen from Eq. (6). Comparing the effect of s when $t = 0$ with the

Experiments with mutation rates ranging from 10^{-2} to 10^{-5} gave similar results to those shown. Without institutions, p remains low, while with both institutions,

(footnote continued)

effect of t when $s = 0$, we see that the former is b/c times the latter and $b > c$ because the altruistic behavior is group-beneficial. (In our simulations, $b = 2$ and $c = 1$ so the s -effect is twice the t -effect.) Also, note that from Eq. (5), if $s_j = c/b = 1/2$, $\Delta p_j = (1 - p_j)(1 - t_j)(s_j b - c) = 0$, but the value of t required to halt within-group selection against the A’s is 1. (In the quadratic cost function we used, the costs of $t = 1$ are four times the cost of $s = 1/2$.)

the average of p in five simulations of 100,000 generations each (for mutation rates of 10^{-2} , 10^{-3} , 10^{-4} , and 10^{-5}) exceeds one half. The average p for the five simulations with a mutation rate of 10^{-5} ranged from 0.75 to 0.83, in each case a sharp rise in p occurred between the 17,150th and 25,855th generation, and high levels of p were sustained throughout the rest of the simulation. The waiting time before a take-off depends on the time it takes for a single group to accumulate a significant number of altruists. This waiting time would be shortened considerably where there are more than 20 groups. Because we set $p=0$ at the initial generation, very low rates of mutation (less than 10^{-5}) sustain low levels of p over very long periods; when, as very occasionally occurs, p rises to high levels it is sustained over very long periods.

4. Early human environments

Does this model illuminate the process by which human group-beneficial behaviors and group level institutions might have evolved? The answer must depend on whether the parameter space in which this co-evolutionary process occurs in our simulations approximates the relevant environment, namely the first 50,000 or 100,000 years of modern human existence, prior to the dramatic transformation of social structure accompanying the advent of agriculture around 11,000 years ago.

Little is known about the relevant late Pleistocene environments, and the difficulty in making inferences about the social organization of human groups during this period on the basis of contemporary simple societies is well-known (Foley, 1987, Kelly, 1995). We can say with some confidence, however, that during much of this period climate was exceptionally variable and that small mobile foraging bands composed of both kin and non-kin, and lacking complex political organization were a common form of social organization (Richerson et al., 2001.)

Our benchmark value for group size, 20, is based on an approximation of the median of the 235 hunter gather groups recorded in Binford (2001), namely, 19. Our handling of group size is not entirely realistic, however. Recall that small size contributes to group-selection pressures by increasing the between-group variance arising when groups that win conflicts double in size and divide. In reality, group fissioning is not by a random draw, but rather appears to be a highly political conflict-resolving process in which kin and coalitions are likely to remain together. Thus fissioning contributes to between-group variance and to reduce within group variance in ways which our model does not capture. A study of fissioning among Amazonian peoples (Neves, 1995, p. 198) reports that “fissioning ... keeps close kin

together but separates them from more distant kin... the potential line of cleavage is furnished by the division in patrilineages.”⁶

As the bearers of the group-beneficial trait are likely to be numerically and socially dominant in the winning group, they may practice what Hamilton termed associative division by segregating bearers of the “other” trait insofar as recognition of traits or characteristics correlated with traits allows. Were this the case, it seems likely that much larger group sizes would sustain the evolutionary processes indicated above though we have not simulated an associative fissioning process.

Very little is known about group conflict during early human history. We do know that deaths due to warfare constitute a substantial fraction of all deaths in many of the pre-state societies in the ethnographic and archeological record. The average reported by Keeley (1996) for ethnographic studies of pre-state societies is 0.19, and for pre-state societies studied by archeologists is 0.16. This compares with estimates well below 0.1 for Europe and the US in the 20th century, 0.03 for 19th century France and 0.02 for Western Europe in the 17th century. A 50-year record of 200 wars among the Mae-Enga in New Guinea, for example, took 800 lives from a population of about 5000, resulting in an annual death rate from warfare (0.0032 deaths per year per head), double that of Germany and Russia in the 20th century but well below the average of the pre-state societies on record (Keeley, 1996, p. 195). Whether these extraordinarily lethal episodes were common during the Late Pleistocene is difficult to say. But some speculations are possible based on what we know about climate change and the migrations that this induced. Boehm (2000, p. 19) writes:

.. 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.

Ember (1978) collected data on the frequency of warfare among 50 foraging groups in the present or recent past. Excluding those who practice some herding or sedentary agriculture, 64% of the groups had warfare every 2 years or more frequently. Even excluding those more bellicose groups who either had horses or relied on fishing, warfare is described as “rare” in only 12% of the groups.

While movement between ethno-linguistic units was probably quite rare, it seems likely that substantial rates

⁶Chagnon (1983, pp. 141–143) studied a Yanomamo village that subdivided and found that average relatedness in the pre-fission village was lower than either of the newly formed units.

of migration among the bands making up these units occurred. Migration rates for the 13 societies surveyed by Rogers (1990) averaged 22% percent a generation with the maximum (the !Kung) less than one half. As Rogers' data refer to somewhat larger than band-sized groups, these data may understate the rate of migration somewhat.

5. Conclusion

We have described a process whereby institutions such as resource-sharing and segmentation provide an environment within which an individually costly group-beneficial trait may evolve, and in which these institutions proliferate in the population because of their contribution to the evolutionary success of the group-beneficial trait. Our simulations have shown that if group-level institutions implementing resource sharing or positive assortment within groups are free to evolve, group-level selection processes support the co-evolution of group-beneficial individual behaviors along with these institutions, even where these institutions impose significant costs on the groups adopting them. In the absence of these group-level institutions, however, group-selection pressures support the evolution of group-beneficial traits only when intergroup conflicts are very frequent, groups are small, and migration rates are low.

Notwithstanding the highly speculative nature of these inferences, it seems possible that the social and physical environments of the late Pleistocene may fall within the parameter space supporting the co-evolutionary trajectories illustrated in Fig. 6. If so, the multi-level selection model with endogenous institutions may provide at least a partial account of the evolution of individually altruistic behaviors as well as group level resource sharing, segmentation and perhaps other institutions during this critical period of human evolution. An implication, explored elsewhere is that altruistic behaviors and warfare as a group practice may have co-evolved, the frequency of warfare contributing to the evolutionary success of altruism, and the presence of a significant fraction of altruists in a group contributing to a group's war-making capacity.⁷

The main causal mechanisms of the model—institutionalized resource sharing among non-kin and intergroup conflict in particular—suggest a central role for uniquely human cognitive, linguistic and other capacities in this process, perhaps helping to account for the distinctive levels of cooperation among non-kin

practiced by humans. The same observation suggests the limited applicability of the model and simulations to most other animals. However, for species in which neighboring groups including unrelated members compete for resources or in which group extinctions are common, a similar model might apply. In these cases individually costly group-beneficial behaviors may contribute via group size or in other ways to the success of the group in avoiding extinctions or in gaining resources from neighboring groups. Examples include social mammals such as the cooperative mongoose *Suricata suricatta*, for which group extinction rates are inversely correlated with group size and in some years exceed half the groups under observation (Clutton-Brock et al., 1999). Similarly, fire ants (*Solenopsis invicta*) and a large number of other ant species form breeding groups with multiple unrelated queens and practice brood raiding and other forms of hostility toward neighboring groups, with success positively related to group size (Bernasconi and Strassmann, 1999). Whether the levels of cooperation observed in these and other species might be explained in part by the causal mechanisms at work in our model is an interesting question which we have not explored.

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⁷A simulation similar to that reported in Fig. 5, for example, shows that if low values of p made conflicts unlikely and conversely, the population spends most of the time (over a very long run) with either high levels of both p and k , or low levels of both (Bowles and Choi, 2003b).

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