
The Coevolution of Institutions and Behaviors

...Selfish and contentious people will not cohere, and without coherence, nothing can be effected. A tribe possessing...a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other...would spread and be victorious over other tribes...Thus the social and moral qualities would tend slowly to advance and be diffused throughout the world.

Charles Darwin, *The Descent of Man* (1982[1871]) p. 156

7.1 Introduction

Few students of human populations doubt that institutions, nations, firms, bands, and other groups are subject to selective pressures. The emergence and diffusion of the centralized, tax-collecting and arms-bearing national state as a form of territorial governance during the past half millennium is an example. The national state became the dominant form of governance because it won wars and induced preemptive emulation among those threatened with military subjugation (Tilly 1975, Bowles and Gintis 1984, Bowles 2004). Similar arguments may explain the evolutionary success of other social arrangements—markets, monogamy, private property, worshipping supernatural beings, social ranking, and sharing the necessities of life among non-kin, for example. These have been ubiquitous over long periods of human history and have emerged and persisted in highly varied environments. Talcott Parsons (1964) termed these arrangements *evolutionary universals*, the most likely explanation of which is that societies adopting them prevailed in competition with other groups. Frederick Hayek (1988) referred to the markets and private property nexus—his “extended order”—in a similar vein, attributing its success to cultural group selection.

Intergroup competition and culturally transmitted group differences in institutional structure are thus central to our explanation of the evolution of cooperative behaviors among humans. We stress intergroup competition for empirical reasons: group conflict and the extinction or subjugation of loser populations have been among the most powerful forces contributing to the emergence, proliferation and persistence of novel human behaviors in

the spread of behavioral traits. The institutions we model are the commonly observed human practices of resource sharing among group members beyond the immediate family. Our model could easily be extended to study other group level institutions, such as monogamous mating practices that, like resource sharing, reduce the within-group variance of material and hence reproductive success.

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 (Lewis 1969, 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 (Kaplan and Gurven 2005). Individuals approve of sharing norms because they are beneficial to group members, and those violating these norms may bear fitness costs of ostracism and shunning, 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.

The inheritance of group-level institutions results from a cultural transmission process based on learned behaviors. When 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 study institutional evolution in ways analogous to the evolution of individual traits (§2.2). Just as the individuals in our model are the bearers of genes or socially learned individual behaviors, groups are the bearers of institutions, and a successful institution produces many replicas, while unsuccessful ones are eliminated. Replication of institutions may take place when a successful group grows and subdivides, forming two groups, or when a group with unsuccessful institutions succumbs to a military, ecological or other challenge and its vacated site is occupied by a colonists from a neighboring group

The evolutionary mechanisms involved in this account are multilevel selection processes with the features that both genetically transmitted influences on individual behaviors as well as culturally transmitted group-level institutional characteristics are subject to selection, with intergroup conflicts playing a decisive role in multilevel selection. The model is thus an example of a gene-culture evolutionary process introduced in Chapter 2, with institutions playing the role of niches—constructed environments affecting the processes of selection acting on genetically transmitted traits (Odling-Smee et al. 2003). We will show that these niches may allow a genetically transmitted altruistic predisposition to evolve, and the resulting altruistic behaviors contribute to the competitive survival of those groups in which these niches have been constructed. This coevolutionary process may account for the emergence and proliferation of other-regarding behaviors under empirically plausible conditions.

As in Section 4.7, we consider an individually costly but group-beneficial trait. Other altruistic traits could be modeled in a similar manner. Included are individual contributions in an n -person public good interaction—common defense, insurance, or the punishment of those who fail to contribute in such situations, and other ways that cheating is sanctioned (Clutton-Brock and Parker 1995, Boyd et al. 2003). As in the previous chapter, we seek to determine the environments in which such a trait, if initially rare, could proliferate and remain at substantial frequencies in a population.

This chapter departs in three ways from the material presented thus far. The first, already mentioned, is our introduction of culturally transmitted group institutions and their analysis in a gene-culture coevolutionary model. Second, we use a group selection model based on selective extinction, and show that it provides a much more plausible account of the evolution of altruism than does the selective emigration model considered in Section 4.7. Finally, the plausibility of groups selection models is an empirical question, so we put our model to an explicit empirical test. We ask: on the basis of archeological, genetic, and other data, is it likely that genetic differences among groups were great enough and that the survival advantages of predominantly altruistic groups were a sufficiently powerful evolutionary force that under the conditions that ancestral humans experienced during the Late Pleistocene and early Holocene, altruism could have proliferated in the way we suggest? Readers interested in more extensive treatments of the empirical estimates and simulations reported here may wish to consult Bowles (2006), Bowles (2007) and Bowles, Choi and Hopfensitz (2003).

7.2 Within-group Variance Reduction

Evolutionary processes are strongly influenced by mechanisms that suppress competition and reduce differences in behavior or other phenotypic variance within entities, whether they be multicellular organisms or groups of ancestral humans. In a paper studying slime mould (*Dictyostelium discoideum*) Steven Frank (1995) writes: “Evolutionary theory has not explained how competition among lower level units is suppressed in the formation of higher-level evolutionary units,” (p. 520) adding that “mutual policing and enforcement of reproductive fairness are also required for the evolution of increasing social complexity.” John Maynard Smith and Eors Szathmary note that many of what they term the “major transitions in evolution” share a common feature: “entities that were capable of independent replication before the transition can replicate as part of a larger whole after it.” (Maynard Smith and Szathmary 1997), p. 6. As a result, the constituent entities making up the higher-level units come to share a common fate, with selection pressures working on the higher- rather than the lower-level units.

Christopher Boehm (1982):421 applied this idea to human evolution. Among ancestral foragers, he wrote, “group sanction emerged as the most powerful instrument for regulation of individually assertive behaviors, particularly those which obviously disrupted cooperation or disturbed social equilibrium needed for group stability.” As a result (Boehm 1999):211: “a ‘political revolution’ experienced by Paleolithic humans created the social conditions under which group selection could robustly support genes that were altruistic.” Relatedly, Irenaus Eibl-Eibesfeldt (1982):177 pointed to the importance of “indoctrinability to identify with values, to obey authority, and...ethical sharing” and thought that “through these bonding patterns, groups become so tightly knit that they could act as units of selection.”

As a result, characteristics of groups such as the institutions that regulate the selective pressures among their members become themselves subject to selective pressures. An example of such a group characteristic—one stressed by Boehm, and we will explore here—are leveling institutions such as monogamy and food sharing beyond the family, namely those which reduce within group differences in reproductive fitness or material well-being. By reducing within group differences, such structures may have attenuated within-group selective pressures operating against individually costly but group-beneficial behaviors, thus giving the groups adopting them advantages in intergroup contests. In this case the ubiquity of group structural

characteristics such as leveling institutions is explained by their contribution to the proliferation of in-group beneficial individual traits and the contribution of these traits to group survival when faced with environmental crises or competition from other groups.

Thus, the formally altruistic (individually costly but in-group beneficial) traits that may proliferate under the influence of multilevel selection include behaviors that may be harmful to members of other groups. The processes modeled here might be best described, paraphrasing Laland et al. (2000):224, as demonstrating the evolutionary success of selfish groups rather than generous individuals. Though our definition of altruism (p. 82) refers only to in-group interactions, in our model individuals interact with outgroup individuals as well: the model works because altruists confer fitness advantages on insiders, while inflicting fitness costs on outsiders. Our references to “group beneficial” behaviors thus refer exclusively to in-group effects.

We thus address two questions: what accounts for the evolution of individually costly and in-group-beneficial forms of human sociality towards non-kin? And what accounts for the differential success those common group-level institutional structures such as states, resource sharing, and monogamy which have emerged and proliferated repeatedly and in a wide variety of circumstances during the course of human history? The coevolutionary process that we model and simulate are based on the idea that the two questions may be more convincingly resolved jointly than singly.

7.3 Selective Extinction

Consider a large meta-population of individuals living in partially isolated sub-populations (called demes). As in Chapter 4, we assume that altruists (A 's) take an action costing c that confers a benefit b on an individual randomly selected from the n members of the deme. The model and notation are summarized in Table 7.3. A 's are bearers of a hypothetical ‘altruistic allele’; those without the allele (N 's) do not behave altruistically. Reproduction is asexual. In the absence of reproductive leveling, individual fitness is identical to the prisoner’s dilemma payoffs in Table 4.2. For example, an A in a group with all A 's will on average receive benefits b and hence will expect a number of offspring surviving to reproductive age, that is $b - c$ greater than the fitness of an N who interacts only with N 's.

We want to determine the conditions under which p , the fraction of A s in the meta-population, will increase. Recall from equation (4.10) that whether

	Equation
(1)	Generic Price Equation (PE): $\Delta p = \text{var}(p_j)\beta_G + \mathbf{E}\{\text{var}(p_{ij})\}\beta_i$
(2)	Generic PE condition for A to increase: $\text{var}(p_j)/\mathbf{E}\{\text{var}(p_{ij})\} - F_{ST}/(1 - F_{ST}) > -\beta_i/\beta_G$
(β_G)	Effect of A on deme-average fitness $\beta_G = dw_j/dp_j = \kappa(dw_j/d\lambda)(d\lambda/dp_j) = 2\kappa\lambda_A$
(β_i)	Effect of A on individual fitness: $\beta_i = dw_{ij}/dp_j = -(1 - \tau)c + b/n + 2\kappa\lambda_A/n$
(4)	Condition for A's to increase (PE): $\Delta p = \text{var}(p_j)2\kappa\lambda_A - \{(1 - \tau)c - (b + 2\kappa\lambda_A)/n\}$
(5)	Condition for A's to increase: $F_{ST}/(1 - F_{ST}) > -\beta_i/\beta_G = \{(1 - \tau)c - b/n\}/2\kappa\lambda_A - 1/n$
(6)	Condition for A's to increase: $F_{ST}/(1 - F_{ST}) > (1 - \tau)c/2\kappa\lambda_A$

Table 7.1. Summary of model and notation. b and c : benefits and costs to deme members; p_k : percent of deme k that are A's; and p : percent of metapopulation that are A's. In the equations, Δp = between deme + within deme; F_{ST} = between-deme variance/total variance; κ = probability of interdemic contest; τ = extent of reproductive leveling; Larger F_{ST} favors A's. Equation 6 says that $F_{ST}/(1 - F_{ST}) >$ individual cost/deme benefits.yyy

altruism evolves ($\Delta p > 0$) depends on the outcome of a race in which the between-group selection process promoting its spread, $\text{var}(p_j)\beta_G$, competes with the within-group selection process tending to eliminate it, $\text{var}(p_{ij})\beta_i$. For the between-deme effect to exceed the within-deme effect (rearranging equation 4.10), it must be that:

$$\frac{\text{var}(p_j)}{\text{var}(p_{ij})} > -\frac{\beta_i}{\beta_G}. \quad (7.1)$$

The right hand side of 7.1 is the ratio of two fitness effects: $\beta_i = dw_{ij}/dp_{ij}$, the effect on i 's fitness of switching from N to A , and $\beta_G = dw_j/dp_j$, the effect on average fitness of members of group j on variations in the fraction group j who are A's. A behavior is altruistic if adopting it lowers one's expected fitness while increasing the average fitness of one's deme (§A4). Given this definition, we are interested in the case where β_i

is negative and β_G is positive. The left hand side of (7.1) is a measure of positive assortment arising from the fact that if the fraction of A 's in demes differ (that is, $\text{var}(p_j)$ is positive), then A 's are more likely than N 's to interact with A 's. Because the within-deme benefits of altruism are randomly distributed, between-deme differences in the prevalence of A 's (i.e. $\text{var}(p_j) > 0$) is the only reason why A 's are more likely than N 's to interact with A 's, and thus to benefit mutually.

But, if A 's are likely to benefit for this reason, they are also more likely to compete over deme-specific resources (Taylor 1992, Wilson et al. 1992). In the selective emigration model of Chapter 4 we allowed the predominantly altruistic demes to grow without these resource constraints. But, here we assume the most stringent form of local density-dependent constraints on reproductive output: sites are saturated so that territorial expansion is required for deme growth. Thus altruism can proliferate only by helping a deme to acquire more territory, not by any of the other ways that members of predominantly altruistic demes might produce more surviving offspring.

Selective extinction may allow the evolution of altruism if predominantly altruistic demes are more likely than other demes to survive between-deme contests and to colonize and repopulate the sites vacated by demes that fail (Aoki 1982). This process is captured by the term β_G , the size of which is determined by the frequency of contests, the fitness effects of surviving a contest, and the contribution of altruists to surviving. In every generation with probability κ each deme engages in a 'contest.' A contest may be a hostile encounter or an environmental challenge without direct deme interaction. Demes that fail are eliminated and surviving demes repopulate the vacated sites.

Demers are the same size (normalized to 1) except that demes that have occupied the site of an eliminated deme are momentarily of size 2 (and eliminated demes are of size zero). The surviving deme then divides, forming two daughter demes of equal size. Let the probability that the deme survives be λ . The size of deme j next generation is thus 1, 2 or 0 with probabilities $1 - \kappa$, $\kappa\lambda$ and $\kappa(1 - \lambda)$, respectively, so expected size is $w_j = 1 - \kappa + 2\kappa\lambda$. The effect of the prevalence of A 's on the expected size of the deme next generation; that is, $\beta_G = dw_j/dp_j$ is the likelihood of a contest (κ), times the effect on deme size of surviving or not (2), times the effect of the prevalence of A 's on the probability of a deme surviving should a contest occur (λ_A); so $\beta_G = 2\kappa\lambda_A$. There is no way to estimate λ_A empirically, so we explore two alternative values: $\lambda_A = 1$ is derived from a model in which all- A and all- N

demes (respectively) survive and fail with certainty should a contest occur; while if $\lambda_A = 1/2$, an all- A deme survives with probability $3/4$ and an all- N deme survives with probability $1/4$. These two alternatives are shown in Figure 7.1.

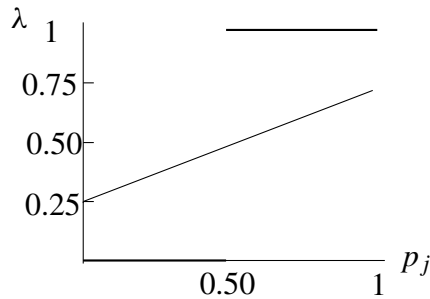


Figure 7.1. Survival probability for deme j if half of the members of the paired group (q) are A 's. Varying p_q shifts the linear function vertically without changing its slope ($1/2$) and shifts the step function horizontally so that if p_q is uniformly distributed over the unit interval, then $d\lambda/dp_j = 1$.

7.4 Reproductive Leveling

Distinctive human practices within groups also created a favorable niche for the evolution of altruism. Individual differences in size, health, behavior, and other influences on access to scarce resources are typically reflected in differences in reproductive success. Among some other primates (Noe and Sluiter 1995, Pandit and van Schaik 2003) and especially among humans, reproductive leveling attenuates this relationship. Because altruists in the model receive lower payoffs than other deme members (by the definition of altruism), they benefit from reproductive leveling, resulting in a reduction of the term β_i .

To see how this works, suppose a particular N were instead an A . In the absence of reproductive leveling and intergroup competition its fitness would be less by an amount c . But the individual who switched from N to A would also have a $1/n$ chance of interacting with itself, garnering the randomly assigned benefit b . Additionally, by switching from N to A , the individual contributes directly to its fitness in another way: by increasing the chance of survival of the deme, in which case, like every member of the surviving deme, it will be doubled. The additional direct effect is the effect

of the switch from N to A on p_j ($1/n$) times the effect of variations in p_j on deme-average fitness (β_G). Thus

$$\beta_i \equiv \frac{dw_{ij}}{dp_{ij}} = -c + \frac{b}{n} + \frac{2\kappa\lambda_A}{n}.$$

Reproductive leveling can now be introduced as a convention, conformity to which is in the interest of each deme member. Reproductive leveling takes the form of a proportional deduction at rate τ of each members' payoffs, the proceeds of which are distributed equally to all members. An example would be 'common pot' food sharing in which some fraction of the food available to a group is pooled irrespective of who acquired it, and then distributed in equal shares to each member. The effect is to reduce within-deme fitness differences between A 's and N 's from $-c$ to $-(1 - \tau)c$, so taking account of all of the direct effects of a switch from N to A on the actors fitness we have.

$$\beta_i = -(1 - \tau)c + \frac{b}{n} + \frac{2\kappa\lambda_A}{n}. \quad (7.2)$$

In keeping with our representing the A 's as altruistic, β_i is negative over the parameter ranges introduced below and in the subsequent simulations. Figure 7.2 reproduces the information in Figure 4.4 but suppresses the baseline fitness, and 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 one's own type, that equalizes expected payoffs is no longer $P(A|A) - P(A|N) = F^*$ as shown in Figure 7.2, but is now $P(A|A)' - P(A|N)' = F' < F^*$. Comparing the two figures one sees that $F^* = c/b$ while $F' = c(1 - \tau)/b$. As a result, were the population structure as in Figure 7.2 (F^*) and the sharing institution in place ($\tau > 0$), then $\omega^A > \omega^N$, so p will increase.

Substituting these values for β_i and β_G into the Price equation 4.10, we have

$$\Delta p = \text{var}(p_j)2\kappa\lambda_A - \text{var}(p_{ij})\{(1 - \tau)c - (b + 2\kappa\lambda_A)/n\}. \quad (7.3)$$

We will assess this condition with genetic data from recent hunter-gatherer populations, using a commonly measured statistic from population genetics, the fraction of the total genetic variance at a locus that is between groups, also known as Wright's inbreeding coefficient (Wright 1922):

$$F_{ST} = \frac{\text{var}(p_j)}{\text{var}(p_j) + \text{var}(p_{ij})}.$$

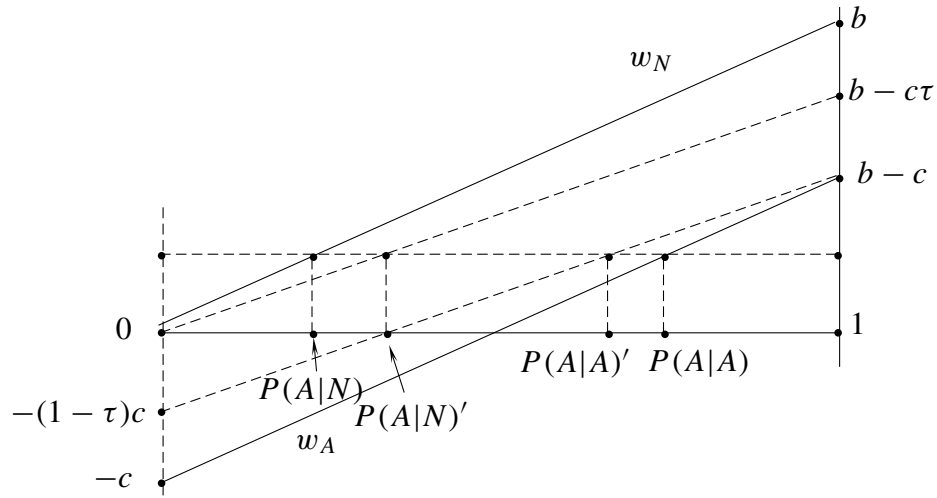


Figure 7.2. Resource Sharing Increases the Relative Importance of Population Structure in the Evolution of an Altruistic Trait. Note: The horizontal axis measures the probability of being paired with an A. The dashed payoff functions indicate the effect of within-group resource sharing. For the value of τ illustrated here, the altruistic trait will proliferate if $F > P(A|A)' - P(A|N)'$ while for $\tau = 0$, $F > P(A|A) - P(A|N)$ is required. For the case of nonrandom pairing (to be introduced below in the simulations reported in §7.7), the analysis is similar, with $b - c\tau$ on the right vertical axis replaced by $(1 - \zeta)b$ and $-(1 - \tau)c$ on the left axis replaced by $\zeta b - c$.

. Using this definition, we rewrite equations 7.2 and 7.3 and find that the A's share of the meta-population will increase if

$$\frac{F_{ST}}{(1 - F_{ST})} > -\frac{\beta_i}{\beta_G} = \frac{(1 - \tau)c - b/n}{2\kappa\lambda_A} - \frac{1}{n}. \quad (7.4)$$

If n is large, this is approximated by

$$\frac{F_{ST}}{1 - F_{ST}} > \frac{(1 - \tau)c}{2\kappa\lambda_A}. \quad (7.5)$$

Like Hamilton's rule for the evolution of altruism by inclusive fitness, this model thus yields a condition indicating the minimum degree of positive assortment necessary to allow altruism to proliferate. The left hand term is analogous to Hamilton's r , the degree of relatedness, but here positive assortment arises solely from between-deme differences in the prevalence of

A 's, not from the tendency of recent descendant kin to interact preferentially. The right hand terms in equations 7.4 and 7.5 are the ratio of individual costs to group-level benefits (analogous to c and b respectively in Hamilton's rule).

We now ask if ancestral humans are likely to have lived under conditions such that equations 7.4 or 7.5 would be satisfied. Table 7.3 is a summary of the main parameters and the estimated range of empirically plausible values.

7.5 Empirical estimates of F_{ST}

Wright (1950):203 speculated that an equilibrium F_{ST} among human groups—namely that which would balance the offsetting effects of migration and drift—might be about 0.02, a value that would preclude inter-demic competition as an important evolutionary force. For example, in the selective emigration model an F_{ST} of this magnitude would require b to exceed c by a factor of 50 in order for altruism to evolve (equation 4.15). But, most empirical estimates of F_{ST} values are considerably larger. The measures of genetic differentiation in Table 7.2 are from recent foraging populations whose population structure, geographical and linguistic proximity, and livelihood may resemble foraging bands of the late Pleistocene and early Holocene (about 150 to 10 thousand years before the present). These estimates are based on genetic material most of which was collected prior to the mid 1970s and in most cases are averages over a large number of genetic systems and over F -statistics among a large number of sub-populations. A nested 3-level hierarchy of measures of genetic differentiation is estimated, depending on the size of the sub-population units: F_{DG} measures genetic differentiation among demes (D) in the same ethno-linguistic group (G), while F_{GT} and F_{DT} , respectively, measure differentiation among groups and demes in a meta-population (T). If most competition is between demes across ethno-linguistic boundaries, then F_{DT} is the relevant statistic.

The median and mean values (respectively) are 0.076 and 0.081. The median and mean for the F_{DT} estimates are 0.081 and 0.093. We think it is unlikely that Table 7.2 overestimates the relevant degree of genetic differentiation among early humans. First, extreme climate variability during the late Pleistocene (Figure 8.1) probably induced frequent deme extinctions, population crashes and subsequent growth, resulting in the colonization of new sites by small groups from a surviving deme. Natural experiments, for example with the plant *Silene dioica* (Giles and Goudet 1997), suggest that the effect may be a considerable elevation of between-group genetic vari-

<i>Population</i>	<i>Index</i>	<i>F</i>
Indigenous circumpolar Eurasian populations	F_{DT}	0.076
Native Siberian populations	F_{DT}	0.170
Native Siberian populations	F_{DG}	0.114
!Kung demes (Southern Africa)	F_{DG}	0.007
Southern African groups	F_{DG}	0.075
Southern African demes (from 18 groups)	F_{DG}	0.081
Aboriginal Australians (12 groups)	F_{GT}	0.042
Kaiadilt-Lardiil groups (Australia)	F_{DT}	0.081
Asmat-Mappi (Lowland Western New Guinea)	F_{DT}	0.056
Mbuti (Central Africa)-San (Southern Africa)	F_{GT}	0.149
Aka (Central Africa) (between groups)	F_{GT}	0.057
Aka (between 'villages' in the same group)	F_{DT}	0.042
Aka (between 'villages' in all groups)	F_{DT}	0.097

Table 7.2. Genetic differentiation among 13 hunter-gatherer sub-populations. The median and mean values (respectively) are 0.076 and 0.081. The median and mean for the F_{DT} estimates are 0.081 and 0.093. Source: Bowles (2006,2007).

ance. Second, genetic differentiation among a subspecies of chimpanzees (*Pan troglodytes schweinfurthii*) whose spatial distribution and demographic history may resemble early humans (Goldberg and Ruvolo 1997) is substantially higher than the median of the estimates in Table 7.2 ($F_{ST} = 0.102$).

However, estimates of genetic differentiation at the locus of an allele that is expressed in an altruistic behavior may differ from estimates based on neutral loci (those not under selection) such as those in Table 7.2. First, an altruistic allele would be, by definition, under directional selection. This would be expected to reduce inter-demic genetic differentiation at least in the very long run, because in the absence of offsetting effects, the frequency of the A 's in the population will eventually go to zero. However this tendency may not work over time scales relevant to human demes. Simulations show that even for very strong selection against the A 's and for plausible initial distributions of A 's in demes, the F_{ST} rises for tens of generations. For moderate selection against the A 's, the F_{ST} may rise for more than a hundred generations before falling. Because fission and extinction events that enhance inter-demic variance are likely to be an order of magnitude more

frequent than this, it appears that high levels of F_{ST} could persist indefinitely. Additional simulations show that exceptionally strong directional selection against the A 's ($c = 0.1$) is compatible with the indefinite maintenance of high levels of F_{ST} , even with random fission.

Second altruists will sometimes be able exclude non-altruists' from their demes (Wilson and Dugatkin 1997), resulting in what Eshel and Cavalli-Sforza (1982) called 'selective assortment.' Directed migration (Rogers and Jorde 1987) will also enhance between-deme variance and reduce within-deme variance. Here, selective assortment is contingent on past behavior that is itself an observable expression of the altruistic allele. As a result, the only way an N can mimic the A 's so as to evade their choosiness is to adopt the altruistic behavior itself and thus to bear its costs. Thus the instability arising in the case of assortment by 'green beards' (Ridley and Grafen 1981) does not arise.

But, there is nonetheless an impediment to selective assortment that is sometimes overlooked: exclusion of N 's is likely to be costly for the A 's, while the associated benefits are shared by all deme members. However, it is not implausible that altruists would undertake some moderate level of N -exclusion as a contribution to the public good. As we have seen in chapter 6, there is ample ethnographic evidence that foragers practice selective assortment when they ostracize or shun individuals who violate behavioral norms. Moreover, our models and simulations (Bowles and Gintis 2004a) confirm that these practices can proliferate when rare and persist indefinitely in a plausible evolutionary dynamic. Finally, it is readily shown (Bowles 2006) that a modest amount of selective assortment generates substantial levels of between-deme differences.

7.6 Deme Extinction and the Evolution of Altruism

While the effects of most forms of reproductive leveling cannot be estimated, the degree of within-deme resource sharing is known from empirical studies of the acquisition and consumption of nutrition among foragers. On this basis we take $\tau = 2/3$ as a plausible benchmark with one-third an alternative value. The appropriate value of n is the number of deme members of a breeding generation (about a third of the census size). Individual bands may have competed for survival, but it is likely that bands in coalition also engaged in contests. Here we take 96 members as a benchmark size, or $n = 32$ members of a single generation. We will also consider very large (strictly,

infinite) demes. Plausible values of c and b will depend on the particular altruistic behavior in question. For example, a warning call would have a different b and c than defending the community against hostile neighbors. To facilitate the exploration of a variety of altruistic behaviors, we present results for a given $b = 0.05$ and c varying from 0 to 0.08. Equations 7.4 and 7.5 make it clear that for sizable demes b is of little importance.

The extent of hostile group interactions during the late Pleistocene and early Holocene may be suggested by climatic data, hunter-gatherer demographics, archeological evidence, and recent histories of foraging peoples, and is a matter of some debate. The evidence is discussed in detail in the next chapter. Early human demes probably faced frequent inter-group, environmental, and other challenges resulting in occasional fatalities or territorial losses or gains, more closely resembling boundary skirmishes among chimpanzees (Watts, Muller, Amsler, Mbabazi and Mitani 2006) than this all-or-nothing deme-extinction scenario.

However ‘pitched battles’ did occur among foragers, as in the conflict between two coalitions of aboriginal Australians involving around 700 combatants (Lourandos 1997):59,61. Environmental shocks may also led to the dispersal or extinction of groups. It seems likely that during some periods of the Pleistocene and early Holocene, intergroup hostility and environmental challenges were frequent and exceptionally lethal. In the next chapter we show that the level of on-going hostility may have resulted in the equivalent of a contest in which the loser is eliminated occurring every five or seven generations. Here we use the lower estimate.

The above estimates are summarized in Table 7.3. They are subject to substantial error given that they are inferences about conditions occurring tens of thousands of years ago for which very little direct evidence is available. With this caveat in mind, suppose early human demographics and social practices resulted in genetic differentiation at the locus of an altruistic allele that was the magnitude of the median in Table 7.2 (0.076). For the benchmark values of τ , n , and λ_A , the solid lines in Figure 7.4 give the combinations of c and κ such that equations 7.4 and 7.5 are satisfied as equalities. More frequent contests or less costly forms of altruism (points above the line) allow altruism to proliferate. Dashed lines do the same for more stringent alternative parameter values. For example, for the estimated κ , if $c = 0.05$, altruism proliferates under both survival functions and the benchmark assumptions, but not for very large demes with limited reproductive leveling.

<i>Determinant</i>		<i>Range explored</i>	<i>Comment or Method of Estimation</i>
Inter-demic genetic differentiation	F_{ST}	0.007-0.17; 0.076	Genetic markers (recent foragers)
Reproductive Leveling	τ	0.66 , 0.33	Food sharing (recent foragers)
Gains-losses from contests per generation	ω	0.30 , (0.40)	Archeological and ethnographic evidence
Per generation probability of a decisive (2,0) contest	κ	$= \omega/2$	Based on Estimates of mortality in on-going conflict
Effect of percent altruists on deme survival	λ_A	1/2, 1	Arbitrary (see Figure 7.1)
Effective deme size (one generation)	n	32 , ∞	Coalition of bands
Cost to Altruist	c	0.0 to 0.08	Depends on behavior under consideration
Benefits to deme (w/o a contest)	b	0.05	As immediately above (virtually no effect)

Table 7.3. Parameter estimates. Benchmark values are in bold. Entries not in bold are alternative values (= 0.4 not used).

For many of the populations in Table 7.2 and for plausible parameter values, then, genetic differentiation is such that even very infrequent contests would have been sufficient to spread quite costly forms of altruism. Because the initial spread of altruism among humans could have been propelled by just a few of the vast number of late Pleistocene demes, the above data and reasoning suggest that selective deme extinction may be part of the account of the evolution of altruism. This is likely in the presence of significant levels of reproductive leveling, but not in its absence, suggesting an important role for culturally transmitted practices in creating a niche in which a genetic predisposition to behave altruistically might have evolved, and perhaps accounting for the distinctive aspects of human altruism not found in other species.

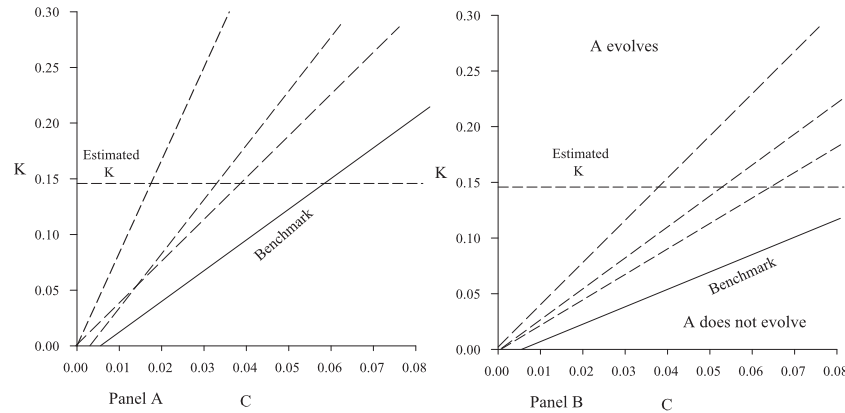


Figure 7.3. Conditions for the evolution of altruism by selective extinction and reproductive leveling. The solid lines are the benchmark values estimated in the text $n = 32$, $\tau = 0.66$. Line 1: $n = 4$, $\tau = 0.33$; Line 2: $n = 32$, $\tau = 0.33$. Line 3: $n = 4$, $\tau = 0.66$. Points above the each line give combinations of c and κ such that altruism would proliferate according to equations 7.4 and 7.5. Panels a and b (respectively) use $\lambda_A = 0.5$ and $\lambda_A = 1$. For both panels, $b = 0.05$. Similar analysis for all of the data in Table 7.2 is presented in Bowles (2006).

Moreover, inter-demic selection could be a substantially greater influence on the evolutionary dynamic than is suggested by the figure. The reason is that the distinctive human aspects of human social interaction facilitating the evolution of altruism frequent lethal inter-group competition and resource sharing differ from group to group. Predominantly altruistic groups are more likely than other groups to exhibit these features and to impose them on vacated sites as we have seen. But, we have not yet modeled the dynamic of genes and group level institutions. Thus far we have posited empirically plausible levels of warfare and reproductive leveling, rather than explained their evolution.

Below and in the next chapter, we will model the coevolution of altruism with these distinctive human institutions. Because this process involves highly complex selection processes operating at two levels in which the magnitude of within group and between group selection effects are endogenously determined by the evolution of group-level institutions, the dynamic

is not amenable to mathematical analysis using the Price equation, or indeed any other mathematical formulation capable of analytical solution. An agent-based simulation (§A1), however, is illuminating.

7.7 The Coevolution of Institutions and Altruism

Our objective in this section is to see if the culturally transmitted group-level institutions that support the evolution of the ‘altruistic allele’ could themselves have evolved even if maintaining these institutions imposed costs on the groups adopting them. We will of course consider reproductive leveling. But, we first introduce an additional aspect of group social structure, the tendency of like types to interact within groups more frequently than would occur by chance. The resulting non-random pairing, sometimes called *segmentation*, may occur because of limited dispersal from one’s place of birth, and consequent tendency to interact with siblings and other kin by recent common descent, or because people can sometimes condition their interactions on the type of the other, based on information about past behavior, for example.

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. Let $\zeta > 0$ be the degree of segmentation, that is, the difference in the conditional probability of an *A* meeting an *A* and an *N* meeting an *A* in the within-group pairing. Thus, the probability of an *A* in group j being paired with an *A* is $\zeta_j + (1 - \zeta_j)p_j > p_j$ and the probability of an *N* being paired with an *A* is $(1 - \zeta_j)p_j < p_j$. Then, abstracting from reproductive leveling, the difference in payoffs between *A*’s and *N*’s in the same group is no longer c , but $c - \zeta_j b$. Segmentation thus reduces the fitness disadvantage of altruists because they are disproportionately likely to meet other altruists, while *N*’s are disproportionately likely to meet other *N*’s. If $\zeta > c/b$, *A*’s will on average do better than *N*’s in group j and as a result the *A*’s will not suffer any reproductive disadvantage. To pose the classical (strong) group-selection problem, we assume $\zeta < c/b$. 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 $(1 - \tau)(\zeta b - c)$ from which it is clear that both institutions retard the within-group selection against the *A*’s.

The institutions represented by ζ and τ differ among groups and they also evolve. In our simulations, 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 replicas of a random selection of themselves. The new inhabitants of the site adopt the institutions of the winning group from which they descended. Institutions are also subject to stochastic variation, increasing or lowering τ and ζ 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 in convex in both ζ and τ .

With Astrid Hopfensitz and Jung Kyoo Choi, we simulated an artificial population living in 20 groups (Bowles et al. 2003). We selected an extraordinarily high cost of altruism, $c = 0.1$ and did not allow A 's to benefit from their own prosocial actions; that is, $b = 0.2$ is conferred on some *other* randomly selected group member. Thus within a group, when $\zeta = \tau = 0$, A 's have ten percent fewer offspring than N 's, making these simulations a demanding test of our interpretation. These and the other benchmark values of the parameters in the simulations shown in table 7.4 were chosen on grounds of empirical plausibility. We initiated each simulation with altruists and institutions absent at time zero, to see if they would proliferate if initially rare (the individual and institutional mutation process will introduce some variability in the population).

	Benchmark Values	Range Explored
Mean Group Size (n/g)	20	7 to 47
Migration Rate (m)	0.2	0.1 to 0.3
Probability of Conflict (k)	0.25	0.18 to 0.4
Mutation Rate (e)	0.001	0.1 to 0.000001

Table 7.4. Key Parameters for the Simulation. 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 0.5 while $t \in [0, 1]$. The costs imposed on the group by these institutions are $(s^2 + t^2)/2$.

A typical simulation appears in Figure 7.5. The early rise in p is supported by the chance increase in both ζ and τ (between periods 100 and 150). When p , the fraction of the meta-population who are A 's, reaches high levels (periods 532 to 588, for example) both ζ and τ decline, typically leading to a sharp decline in p . The subsequent rise in s or τ occurs by chance. The 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, which means that $\text{var}(p_{ij})$ takes its maximum value ($\text{var}(p_{ij}) = p_j(1 - p_j)$) so the within-group selection term in the Price equation (4.11) is also at its greatest. As a result, the beneficial effects of retarded within-group selection gained by higher levels of τ or ζ are maximized in this region. By like reasoning, 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 had occupied are then peopled by the descendants of winners, who typically bear lower levels of these institutional variables. As a result, both ζ and τ fall.

We checked to see if the proliferation of the A 's could have been the result of the direct benefits of switching from N to A offsetting the costs in these simulations (as was suggested by Lehmann and Keller (2007)). This seems possible given the reductions in the effective costs associated with the coevolving levels of resource sharing and segmentation. We found that when these institutions are absent ($\tau = 0 = \zeta$), the direct benefits of switching from N to A (associated with increased likelihood of group survival should a conflict occur) were about one eighth of the costs, while when τ and ζ were at the levels they assumed on average in these simulations, the direct benefits rose to perhaps a third of the costs. Thus, the A behavior remained altruistic even under the cost-reducing effects of resource sharing and segmentation.

Could individual level altruism have evolved had group level institutions not co-evolved with it. To answer this question we constrained ζ and τ to be zero in all periods. Altruism failed to evolve over a large number of implementations of this treatment. We 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 the institutions perform no group-beneficial function, thus leading groups that

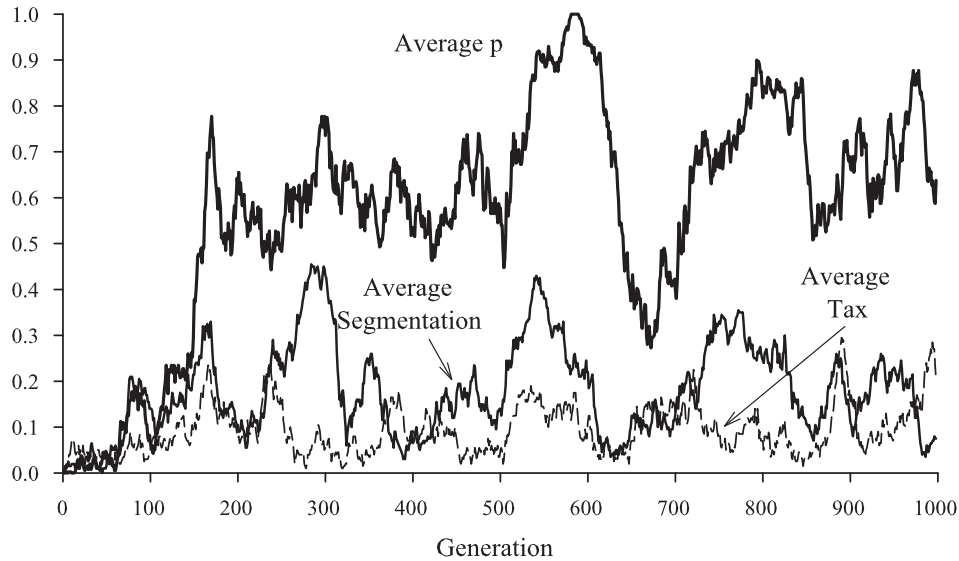


Figure 7.4. The Coevolution of Leveling, Within-group Segmentation, and Altruism. The figure represents 1000 period history of a run using the benchmark parameters from Table 7.3. The population average frequency of altruists is p , while τ and ζ give the average across the 20 groups of the level of resource sharing and segmentation. Altruism and both group-level institutions are initially rare. The particular time frame shown was selected because it clearly reveals this dynamic, which is observed over long periods in many runs.

by chance adopt a high level of sharing or segmentation to lose conflicts in which they are involved.

Finally, we wanted to know how sensitive our simulations are to variations in the key parameters. To do this, 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 (κ) from 0.18 to 0.51. The results appear in Figure 7.4.

The top panel shows that with both institutions constrained not to evolve, a group size of 7 (meaning about 21 individuals, roughly the size of a single foraging band) 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

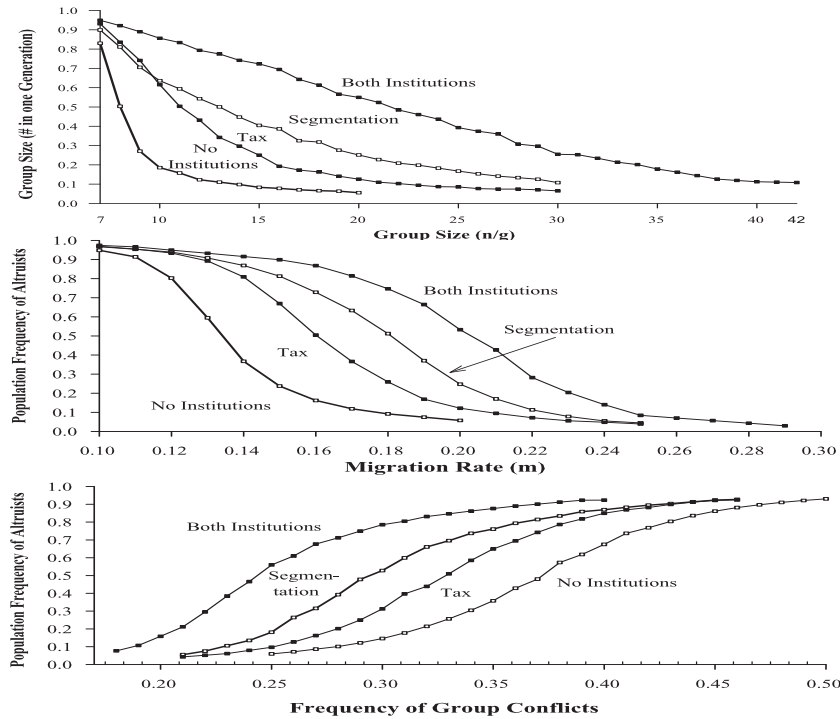


Figure 7.5. Group-level Institutions Increase the Size of the Parameter Space for which Altruistic Behaviors are Common. Each data point is the population average frequency of altruists over 10 runs of 50,000 periods each for the parameter value indicated on the horizontal axis. Each run began with $p = \tau = \zeta = 0$. The curve labeled “none” gives the results for runs in which τ and ζ 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 p .

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. 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 high levels of altruism with significantly fewer between-group conflicts. A “vertical” reading of the figure is also illuminating: for example, the bottom panel shows that for $\kappa = 0.3$, p is less than 0.2 without institutions, but is greater than 0.8 with both institutions free to evolve.

7.8 Conclusion

We have shown that the between group-genetic differentiation, patterns of group extinction and other conditions under which model of selective extinction with reproductive leveling could have worked to proliferate altruism are very likely to have existed at least for some early human groups. We have also described a process whereby institutions such as reproductive leveling and within group 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. Our simulations also suggest that both altruistic behaviors and reproductive leveling institutions could have emerged and proliferated from an environment in which they were initially rare. Recall that p , τ , and ζ are all set to zero at the beginning of our simulations and all three evolve from this initial condition, as in Figure 7.5. Crucial to this process is the fact that food sharing and other forms of reproductive leveling do not require the pre-existence of altruistic preferences: adherence to these conventions is a best response for self-interested individuals. Thus, as we have seen in Chapter 4, a norm that prohibits the powerful from monopolizing food supplies could be sustained by the repeated nature of dyadic network interactions or the adverse reputations that violators would suffer. In light of the significant benefits of co-insurance in the highly variable Pleistocene environments, the conditions outlined in Chapter 4 for the success of reciprocal altruism or indirect reciprocity—frequent on going in-

teractions with public and high quality information—could easily been met, allowing the initiation of food sharing, especially in relatively small groups of highly related individuals. Indeed, as we have seen in Chapter 1, it seems likely that some kind of food sharing is a very early development in human behavior, having co-evolved with the shift to diet based on a large meat packages. Once established the norm could persist in larger, less closely related groups, as Axelrod and Hamilton (1981) showed. Its effect, as this chapter has shown, would be to promote the spread of altruistic preferences including the public spirited punishment of transgressors, thereby stabilizing reproductive leveling even for groups of substantial size.

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 Figure 7.5. If so, the multilevel 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.

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, as we have seen, reproductive leveling occurs in some other species, other forms of within-group variance reduction are also not uniquely human. Moreover, 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, Gaynor, McIlrath, Maccoll, Kansky, Chadwick, Manser, Skinner, and Brotherton, 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.

Group conflict plays a central role in this explanation, but thus far we have not sought to explain either the motives promoting it or the structure of group interactions in which lethal conflict is a likely outcome. This is our next task.