

# The Co-evolution of Individual Behaviors and Social Institutions

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# **The Co-evolution of Individual Behaviors and Social Institutions**

## *Abstract*

We jointly address two puzzles, namely what accounts for the evolutionary success of both: (a) individually costly and group-beneficial forms of human sociality towards non-kin; and (b) those group-level institutional structures such as food sharing and monogamy which have emerged and diffused repeatedly in a wide variety of ecologies during the course of human history. We show that the frequency and consequences of intergroup conflicts may provide an important part of the answer to both questions: in-group beneficial behaviors may evolve if they inflict sufficient costs on out-group individuals while group-level institutions limit the individual costs of these behaviors. We model a co-evolutionary process in which individual traits are transmitted either genetically or culturally and in which the evolutionary trajectories of individual traits and social institutions are mutually determining. Our simulations show that if group-level institutions implementing resource sharing or non-random pairing among group members may evolve, group-level selection processes support the co-evolution of group beneficial individual traits along with these institutions, even where the latter 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. Thus under parameter values which may bear some resemblance to the relevant environments during the first 90,000 years of anatomically modern human existence, in-group-beneficial individual traits and group-level institutions of resource sharing and social segmentation could readily evolve, the sociality of humans thus being in part a consequence of human capacities in social institution building.

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## 1. Introduction

Some common *individual* human practices may have arisen and persisted because individuals in groups where the practices were prevalent enjoyed the group benefits of the practices, even if those engaging in the practices did less well materially than their fellow group members eschewing them.<sup>1</sup> In a much-cited passage Charles Darwin (1873:156) refers to courage, sympathy, and unselfishness as possible examples, these traits proliferating because “a tribe possessing the above qualities in a high degree would spread and be victorious over other tribes.” But if this is the case, it is also likely that common social structural characteristics of *groups* have also emerged and proliferated for similar reasons, that is because they protected those individuals engaging in group-beneficial practices from exploitation by their fellow group members pursuing more selfish strategies and thus favored some groups over others in inter-group conflicts. Group level institutions thus are constructed environments capable of imparting distinctive direction and pace to the process of biological evolution and cultural change.<sup>2</sup> As a result, individual and group characteristics may have *co-evolved*, the distribution of individual traits in a population affecting the evolutionary success of groups with differing social structures, and the distribution of group structures in the population affecting the evolution of the distribution of individual traits.

We thus address two puzzles: 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 co-evolutionary process which we model and simulate are based on the idea that the two puzzles may be more convincingly resolved jointly than singly.

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<sup>2</sup> Institutions thus are examples of niche construction (Laland, Odling-Smee, and Feldman, 2000a, and Bowles, 2000)

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 (Michod (1996), (Ratnieks (1988)). In paper which examines the case of slime mould (*Dictyostelium discoideum*) Steven Frank ((1995a):520) writes: "Evolutionary theory has not explained how competition among lower level units is suppressed in the formation of higher-level evolutionary units," adding that "mutual policing and enforcement of reproductive fairness are also required for the evolution of increasing social complexity." Christopher Boehm ((1982):421) applied this idea to human evolution: "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."

An example of such a group structural characteristic -- one stressed by Boehm, and we will explore here-- 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. By reducing within group differences in individual success (however measured), such structures may have attenuated within-group selective pressures operating against individually costly but group beneficial practices, thus giving the groups adopting them advantages in intergroup contests.<sup>3</sup> 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 success in inter-group conflicts.

Thus the formally altruistic (individually costly but in-group beneficial) traits which may proliferate under the influence of group selection include behaviors which are harmful to members of *other* groups. The opening remark by Darwin (and the example of the diffusion of the European national state below) suggests that he processes modeled here might be best described as demonstrating the evolutionary success of *selfish groups* rather than *generous individuals*.<sup>4</sup> Though the conventional

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<sup>3</sup> We model what we term *resource sharing* and note that while it may be motivated by egalitarian, insurance, or other motives, its effects are to attenuate phenotypic differences within a group.

<sup>4</sup> We are paraphrasing Laland, Odling-Smee and Feldman (2000):224.

definition of altruism refers only to ingroup interactions, in our model individuals interact with outgroup individuals as well: the model works because altruists confer fitness advantages or material benefits on insiders, while inflicting fitness costs or material losses on outsiders. Our references to “group beneficial” or “selfish” behaviors thus refer exclusively to *in*-group effects.

In the next section we explain how an analysis of group conflicts may illuminate the co-evolution of individual behaviors and group-level institutions. We then develop a model of the differential replication of individual traits subject to multi-level selection with group conflicts, extinctions and births.<sup>5</sup> In section 4 we use an agent based simulation to determine the conditions under which an individually costly and in-group beneficial trait can proliferate in the population (the key parameter values concern the frequency of group conflict and individual updating, group size, and intergroup migration.) We then (in section 5) extend the model to take account of between group differences in social structure, showing that both resource sharing and segmentation (positive assortment) strengthen the force of group selection; we use also this extended model as the basis of further simulations in which group-level institutions and individual traits co-evolve.

Our simulations show that if group-level institutions implementing resource sharing or non-random pairing among group members may evolve, group-level selection processes support the co-evolution of group beneficial individual traits along with these institutions, even where the latter 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.

In the concluding section we ask whether this model could explain either the genetic or cultural evolutionary processes operating during the roughly 100,000 years of anatomically modern human existence.

## *2. Group conflicts and multi-level selection*

The evolutionary mechanisms involved in this account are multi-level selection processes with the novel feature that both individual-level behaviors and group-level institutional characteristics are subject to selection and intergroup conflicts play a decisive role. (The underlying model is equivalent to the standard extended fitness accounting framework applied to individuals in groups.) As has been long recognized (Price, 1970, Crow and Kimura, 1970), in populations composed of

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<sup>5</sup> The model is adapted from Bowles (2000).

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. Where the degree of successful replication of a trait depends on the composition the group and where group differences in composition exist, group selection contributes to the pace and direction of evolutionary change. The classic problem of group selection arises when between-group effects favor the proliferation of a group-beneficial trait such as altruism which is disfavored by individual selection within groups.

Few students of human populations doubt that institutions, nations, firms, bands, and other social aggregates may be subject to selective pressures operating at the group rather than individual level (Alchian (1950), Becker (1962), Parsons (1964), Hayek (1990), Tilly (1990)). But at least until recently, most biologists who have modeled evolutionary processes under the joint influence of group and individual selection have concluded that the former cannot offset the latter except where special circumstances heighten and sustain differences between groups relative to within group differences<sup>6</sup>. Thus group selection models are widely judged to have failed in their defining task, namely to explain the evolutionary success of individually costly forms of group-beneficial sociality. As a result, while the biological explanation of group beneficial behaviors has focused on inclusive, kin-based fitness mechanisms, the impressive levels of non-kin based sociality in the case of humans has remained for the most part unexplained.<sup>7</sup>

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<sup>6</sup> Williams (1966), Crow and Kimura (1970), Boorman and Levitt, (1973) Maynard Smith, (1976). The negative assessment of the likely empirical importance of group selection is based on the generally more rapid rate of selection within as opposed to between groups and fact that for many species the main source generation of differences in group (other than genetic relatedness) is drift or random assortment (Crow and Kimura point to "the much larger variance within a group than between group means, the larger numbers that minimize the "noise" from random events, and the slower effective "generation length" for intergroup selection." (1970):242.) But subsequent work suggests that impediments to group selection may be less general than was once thought (Uyenoyama (1979), Uyenoyama and Feldman (1980), Harpending and Rogers (1987)) and may apply with less force to human populations.

<sup>7</sup> These do not exhaust the explanations offered, of course. Zahavi (1995) and Smith, Bowles and Gintis (2000) suggest that group beneficial actions (for example Arabian babblers serving as sentinels, humans engaging in dangerous hunting practices and publically distributing the catch) may directly rewarded by enhanced status and reproductive success. Simon (1990) proposed a mechanism whereby costly but group beneficial behaviors free ride on the individually beneficial behaviors ("docility," or

But as Cavalli-Sforza and Feldman (1973), Hamilton (1975), Boyd and Richerson (1985, 1990), Sober and Wilson (1994, 1998), Wilson and Dugatkin (1997), Boehm (1996, 1997) and others have pointed out, group selection may be of considerably greater importance among humans, given the advanced level of human cognitive capacities, and the resulting substantial influence of cultural inheritance on human behavior and special the nature of human groups. Among the distinctive human characteristics which may enhance the relevance of group selection (of either cultural or genetic variation) is our capacity for the suppression of within group phenotypic differences (egalitarianism, co-insurance, consensus decision making), conformist cultural transmission, forms of social differentiation supporting high levels of assortative interactions, the maintenance of group boundaries, and the frequency of intergroup conflict.

We model a multi-level selection process in which intergroup contests, group extinctions, and the emergence of new groups play a central role in the co-evolution of a group-beneficial individual trait (formally equivalent to altruism) and two group-level structural characteristics, namely resource sharing and segmentation. Two aspects of this model are unusual and deserve comment: the modeling of group-level structural characteristics and the role of group conflict.

First, group differences in institutional structure persist over long periods of time due to the nature of institutions as conventions, namely within group near uniformities of behavior arising from the fact that the relevant actions are mutual best responses conditional on the expectation of similar behaviors by most others. The conventional nature of institutions may account for their long term persistence and also their occasional rapid demise under the influence of shocks.<sup>8</sup> We study institutional evolution in way analogous to the evolution of individual traits: just as the individuals are the bearers of genes or learned behaviors, 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 with the behavioral uniformity among individuals being sufficiently great to treat behavior according to the institution as a group level characteristic. By contrast the differential replication of individual

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"indoctrinability," for example) with which they are pleiotropically paired.

<sup>8</sup> Conventions may also change in response to both stochastic events (Young (1998)) and an interaction of chance and intentional joint action of the members of a group (Bowles (2001) but the focus here is on institutional change induced by interactions with other groups.

traits may be based on either cultural or genetic inheritance.<sup>9</sup> Thus our model depicts a gene-culture co-evolutionary process.<sup>10</sup>

Second, the importance of intergroup contests and cultural or physical extinction of loser populations is suggested by the importance of war in the spread of cultural traits. A notable example is the emergence and spread of an entirely new organizational entity -- the national state -- and the norms supporting it in Europe, and its eventual diffusion throughout the world during the past half millennium.<sup>11</sup> In 1500 roughly 500 sovereign state-like entities existed in Europe governed by a variety of institutions ranging from free cities to religious orders; by 1990 the number had fallen to 28, and a single form -- the centralized national state -- had triumphed. In the two centuries following 1500, there were major 63 wars (defined as involving over 1,000 battle deaths a year, counting only the great powers); with wars occurring so frequently that only ten years were with without one (Tilly, 1990:72).

A multi-level selection account of the diffusion of the national state is the following. The national state evolved because it won wars with competing organizations, and was able to assimilate the defeated populations. The ability to win wars depended on its peculiar ability to mobilize soldiers and other military resources. This ability depended on the extent of commerce and credit, tax compliance, and the willingness to serve rulers in war. These, in turn, were fostered by the diffusion of norms guiding individual behaviors which while not (at least initially) individually advantageous, contributed to group success in war. Candidates for such norms are: voluntary tax compliance, willingness to risk danger in war for a ruler or nation (including loyalty towards insiders and outgroup hostility) and respect for property rights. The norm of monogamy may have played a similar, if less obvious, role in

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<sup>9</sup> We simplify greatly by abstracting from the precise mechanisms of genetic and cultural transmission, and assuming only that trait replication by either means is monotonic in payoffs, namely that the differential material success accruing to different phenotypic attributes of individuals (their behaviors in strategic interactions) results in differential rates of replication of the traits either through differential reproductive success or the tendency of successful phenotypes to be copied through social learning.

<sup>10</sup> Feldman and Cavalli Sforza (1981):362 suggest the possibility of modeling the co-evolution of genes and institutions, and Durham (1991) explores interactions of genes with farming practices in West Africa, marriage patterns in Tibet, and other examples.

<sup>11</sup> I address this case in more detail with the relevant historical sources in Bowles 2000.



securing popular cooperation with the projects of the elite.<sup>12</sup> Each of these norms contributes directly or indirectly to the state's warring capacity, but requires the bearer of the norm to forego possible gains and endure losses (including reduced reproductive success). Successful centralized states assimilated the populations they absorbed, and over the period they promoted and eventually required a common pattern of childhood socialization. The expansion of the European national state to the Western Hemisphere resulted in the virtual elimination of losing populations and the occupation and repopulation of their sites by Europeans.

Other well documented empirical cases of intergroup contests and assimilation are the conquest of the Dinka by the Nuer (Kelly, 1985) and the process of cultural evolution in New Guinea studied by Soltis, Boyd and Richerson (1995). The meteoric spread of Islam in the century following Mohammed's death -- by 750 encompassing a broad swath from beyond the Indus River in the east to the Douro River in Spain in the West -- may also be explained in group selection terms, with, according to Reuben Levy ((1957):3) the faith in Allah providing "a bond far stronger though more subtle than that of kinship," and facilitating more inclusive systems of taxation and military recruitment and alliance. Thus the process of group conflict followed by cultural assimilation or physical extinction which we presently model adopt appears to be quite general.

### *3. Differential replication with group extinctions*

Consider a single trait, which may be absent or present in each individual in a large population whose members each belong to one of a large number of groups. Let  $p_{ij} = 1$  indicate that individual  $i$  in group  $j$  has the trait, with  $p_{ij} = 0$  otherwise. Using a discrete time non-overlapping generations framework, let  $p$  and  $p'$  represent the fraction of the population with the trait during a given and the subsequent time period, respectively, and  $\Delta p = p' - p$ . As is well known, George Price's (1970) general equation for the decomposition of any selection processes can be used to partition  $\Delta p$  into group and individual effects (Grafen, 1985, Rogers, 1990, Frank, 1995b.)

Without specifying the nature of the trait replication and updating process, suppose in any period each individual present in the previous period is represented by

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<sup>12</sup> Herlihy and Klapische-Zuber write: "The great social achievement of the early Middle Ages was the imposition of the same rules of sexual and domestic conduct on both rich and poor" (1985):157. See also MacDonald (1995). While reducing the advantages of the successful and powerful, the norm of monogamy may have been instrumental, as Alexander (1979) and others suggest in allowing the powerful to recruit others to their projects, including war.

some number of exact replicas (if the individual had the trait, the replicas do as well); those favored by the selection process yielding more replicas than those disfavored. Define the selection coefficient  $w_{ij}$  as the number of replicas of individual  $i$  in group  $j$ , and let  $w_{ij}$  depend on  $i$ 's own trait and the frequency of the trait in the group ( $p_j$ ,  $[0,1]$ ) according to :

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

where  $\beta_g$  and  $\beta_i$  are the partial regression coefficients of  $w_{ij}$  on 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  $\beta_0$  is baseline replication. Define  $\beta_G / \beta_g + \beta_i$  as the regression of the group average number of replicas on the frequency of the trait in the group (the difference in the number of replicas made by an individual in a group composed entirely of those with the trait and a group entirely without is  $\beta_G$ ) Then following Price (1970)

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

where  $w$  is the population average selection coefficient (which we normalize to unity) and the expectation operator  $E \{ \}$  indicates a weighted summation over groups (the weights being group size). The first term captures the group selection effect while the second represents the effect of individual selection. (A simple derivation of this decomposition is in Bowles, 2000). It follows that (abstracting from degenerate cases such as zero variances) an interior frequency of the trait will be stationary where these two terms are of opposite sign and equal magnitude (assuming that the regression coefficients and (weighted) variances making up these terms are themselves stationary.) If the second term is negative (as it will be in the case of an individually costly within group beneficial trait) the frequency the trait within all surviving groups will fall over time. But as  $\beta_G$  is positive this tendency will be offset; in the model below the group effect works by the continual extinction of groups with disproportionately low frequencies of the trait and their replacement by "new" groups with disproportionately high trait frequencies. The group structure of a population is a source of non-random pairing even if within group pairings are random; in this respect multilevel selection is indistinguishable from evolutionary processes based on other forms of assortment (kin selection and other forms of within group clustering).

The Price equation describes an equilibrium rather than a complete dynamical system; it thus gives the stationarity condition for  $p$ , but it does not account for the movement of the variances upon which it is based. In most biological models 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. However, for reasons mentioned at the outset, in human populations reproductive leveling and (for culturally transmitted traits) conformism may make between group variances more robust. Where effective group size is small (for example the dozen or fewer family units in a foraging band) and where groups frequently divide either in response to increased size or interpersonal tensions within the group, sampling error will increase between group variance (where group division is deliberate – likes associating with likes, for example – the process of assortative fissioning will further contribute to between group differences.)

One way to determine if these variance enhancing effects are strong enough to make group selection an important influence on evolution is agent based simulation. To do this we present a specific formulation of the general selection process represented by equation (1). Like equation (1) the model does not specify the process of trait replication; differences in the number of replicas made can be modeled either as a process of cultural updating of learned behaviors or differential fitness of genetically transmitted traits. In the case of cultural updating, individuals may switch their traits; and when they do we count this as making zero replicas (and another individual, bearing the newly adopted trait has made two replicas). For genetically transmitted traits we use the standard accounting at the phenotypic level to say that traits determine behaviors and that bearers of different traits may differ in the number of members of the next generation they leave. To avoid over abstraction we describe the model in cultural terms – individuals “switch” or “retain” their learned behaviors -- pointing out where necessary modifications to apply the model to genetically transmitted traits.

The basic setup of the model is as follows. A large population lives in  $n$  groups, interacting with group members in some productive activity and with outgroup members in intergroup contests. Individuals are of type A and N. For concreteness, consider a behavior which costs the individual  $c$  and confers a benefit of  $b$  on a randomly paired (single) member of the group, so a member in a group composed entirely of A's produces  $b-c$  more replicas than that of a member a group with none. As we assume  $b-c > 0$ , the A-trait is group beneficial. Thus using the definitions above,  $\$_i = -c$ ,  $\$_g = b$  and  $\$_G = b-c$ .

Individuals may switch their type under three conditions: i) when they are paired with an individual who captures more of the benefits of their interaction; ii) when their group loses an intergroup conflict and they are assimilated to the winners; and iii) by chance (idiosyncratic updating). Specifically while the given number of individuals are infinitely lived, groups are not, they go extinct, their members absorbed into or replaced by population growth of the more successful groups, and

winning groups subdivide.<sup>13</sup>

Here is the sequence of updating: i) individuals are paired and take actions determined by their type; ii) based on the resulting payoffs, individual updating occurs (some switch while others retain their type); iii) groups are selected and paired for contests and a winner is determined based on the average group-average payoffs; iv) losing groups are assimilated to winners (meaning the frequency of A among the losers is set equal to that of the winners); v) the winning group (enlarged by the assimilation or replacement of losers) divides, thereby restoring the number and size of groups; vi) individuals emigrate and vii) individual updating in the newly constituted groups then occurs (as in (i) above) and the process continues.

Abstracting from idiosyncratic updating (which will be introduced presently) individual level trait replication is described by a standard payoff monotonic replicator dynamic. If the individual traits are culturally transmitted the process is as follows. In every period there is a probability  $T \in (0,1]$  that each member of the population has an opportunity to switch when paired to interact with another member of the group. If the time period is a generation and the trait genetically transmitted, then  $T = 1$ , while for culturally transmitted traits shorter time periods and more frequent updating opportunities may be appropriate. We assume that  $T$  is identical across groups. An individual will switch only if they receive a lower payoff than the other in the pair and will do so with a probability equal to the group average difference in the payoffs to the two types (which is  $c$ ) scaled by the factor  $\zeta_i$  which expresses payoff differences in units of probability of switching.)<sup>14</sup> Thus only A's paired with N's will switch. If pairing is random the fraction of A's in group  $j$  who both have an opportunity to update and are paired with an N is  $T(1-p_j)$  where  $p_j$  is the frequency of A's in group  $j$ . Thus

$$(3) \quad \dot{p}_j = -p_j(1-p_j)Tc\zeta_i$$

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<sup>13</sup> If genetic transmission of traits is concerned losing populations suffer reproductive disadvantage. A simple variant used here is that groups occupy sites with fixed carrying capacity. Both individuals and groups die; all members of losing groups are killed and the site they occupied by a subset of the winning group, and the population of on the two sites grows to restore its pre-conflict size (determined by the carrying capacity of the sites). An equivalent but more general formulation would allow losing groups to remain living as subject peoples in among the winning population while enjoying reduced levels of fitness due to their subordinate status.

<sup>14</sup> An individual who switches produces zero replicas and other of the pair produces two (only one individual in the pair will ever switch).

which can be seen to be one of the  $\text{var}(p_{ij})\$i$  terms in (2) where  $\$i = -Tc(i)$ . Equation (3) can also be rewritten as the familiar replicator dynamic equation

$$(4) \quad dp_j/dt = p_j(B^A - \underline{B})$$

where  $B^A$  and  $\underline{B}$  are expected number of replicas produced by A's and mean number of replicas in the group, respectively.<sup>15</sup> It is clear from (4') that where individual traits are genetically inherited (in a simplified model of asexual reproduction in which phenotypic behaviors are the expression of a single gene) the expected payoffs  $\underline{B}$  may be interpreted as measures of fitness; differences in the expected number of replicas are not based on the probability of switching (by acquiring a new cultural trait through social learning) but simply the expected number of offspring surviving to reproduce.

Turning now to the group effects represented by the first term on the right-hand side of (2), assume that in each period following individual updating, groups are paired for a "contest" which may be military, cultural, economic or some other, this event happening in each period with probability  $\beta$  for each group. If the group is engaged in a contest and wins, it absorbs the other group and assimilates its population, the new population replicating the frequency of the trait of the winning group. As the winning group is now enlarged by the absorption of the losing group, we assume that following the assimilation of the new population, the winning group divides, creating two groups.

We assume that groups are always of the same size (normalized to 1) except that winning groups are momentarily (prior to subdividing) of size 2 (and losing groups are of size zero). Groups that have prevailed in a contest and absorbed another group are by this device counted twice. Thus if group  $j$  is of size one this period then its expected size next period (before any subdivision) depends on the probability that a contest has taken place and the probability of victory in such a contest. Suppose the probability of prevailing in a conflict is equal to its group average payoffs scaled by  $(\beta/2)$  which converts group level payoffs into a probability of victory. Then expected group size following a contest is  $(\beta/2) B_j$  and the expected size of group  $j$  is thus 1, 2 or zero with probabilities  $(1-\beta)$ ,  $\beta B_j (\beta/2)$ , and  $\beta(1 - B_j (\beta/2))$ , respectively or

$$(5) \quad w_j = 1 - \beta + \beta (\beta/2) p_j(b-c) = 1 + \beta (\beta/2) p_j(b-c) - 1$$

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<sup>15</sup> See Bowles (2000) for a more complete derivation. Note that  $\$i$  (the within group difference in the average number of replicas made) is  $B^A - B^N = -Tc(i)$ . The replicator dynamic equation in the text is equivalent to (3) because  $\underline{B} = 1$  and A's make a single replica when paired with an A while switching with probability  $Tc(i)$  when they meet an N, which happens with probability  $(1-p_j)$ , so  $B^A = 1 - (1-p_j)Tc(i)$ .

Thus the effect of variations in  $p$  on the number of replicas of the members of group  $j$ , namely,  $\Delta n_j$  is just  $\Delta n_j = \frac{1}{\sigma} \Delta p_j$ .

Combining (5) with (3) and taking the expectation of the within-group variances, the Price equation (2) is:

$$\Delta p_j = \frac{1}{\sigma} \left( \frac{1}{n} \sum_i q_i \Delta p_i - \frac{1}{n} \sum_i q_i [p_i(1-p_i)] \right) \frac{1}{\sigma} \Delta p_j$$

where  $q_j = w_j/n$ , that is, the expected fraction of the total population who are in group  $j$ . Setting  $\Delta p_j = 0$ , and defining  $F = \frac{1}{n} \sum_i q_i \Delta p_i / \Delta p_j$  and  $\frac{1}{\sigma} \Delta p_j / \Delta p_j$  the stationarity condition for  $p$  is

$$(7) \quad (b-c)/c = F \left( \frac{1}{\sigma} \Delta p_j / \Delta p_j \right)$$

which says that *the ratio of group benefit ( $\Delta G$ ) to individual cost ( $\Delta C$ )* must be equal to the product of the three terms on the right-hand side of (7), each of which is the ratio of a within group to a between group process. These are:

- i)  $F$  the *relative size of the within group relative to the between group variance* of the trait;
- ii)  $\frac{1}{\sigma} \Delta p_j / \Delta p_j$ , the *relative effect of payoffs on success* in individual replication compared to the effects of material benefits in winning group contests; and
- iii)  $\frac{1}{\sigma} \Delta p_j / \Delta p_j$ , the *relative speed of the updating process* represented by the relative frequency with which individuals (compared to groups) have an updating opportunity.

Each of these terms will be affected by the institutions and other structures governing within and between group interactions. Before we consider these effects we will investigate the population dynamics implied by the above model to determine the conditions under which a within-group beneficial trait might proliferate if it were initially rare.

#### 4. *The diffusion of an in-group beneficial trait through group conflict*

In the simulations below a population of (a thousand) individuals are members of groups which are randomly paired for contests in the manner described above, the winner being the group with the higher average payoffs.<sup>16</sup> We consider the

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<sup>16</sup> We executed the simulations using Visual Basic.

“individuals” making up our groups to be family units (namely closely related individuals who migrate jointly and remain together when groups fission.) Migration takes place among the groups at the rate  $m$  per period (we vary  $m$  from 0.1 to 0.4)<sup>17</sup> Within groups individuals are paired and they update (produce replicas) as above except that with probability  $g$  they switch their trait for idiosyncratic reasons, that is for reasons not taken account of by the model (we use a relatively high rate of idiosyncratic replication -- 0.1 in most runs -- but note that lower or higher rates have little qualitative effects on the outcomes). For concreteness the period of time may be considered a half a generation: if the probability that an individual has an updating opportunity,  $T = 0.5$  this means that updating occurs once per generation. Analogously if the probability that a group is paired for a contest,  $\beta = 0.5$ , group contests occur roughly once in a generation. We use these values of  $T$  and  $\beta$  as well as considerably higher values of  $T$  and lower values of  $\beta$  in subsequent runs. We will consider the historical relevance of these parameter values in the conclusion. In all our simulations we set  $p=0$  at  $t=0$ .

We first sought to determine if under quite favorable conditions (small groups, limited inter-group migration and frequent intergroup contests) the group-beneficial trait could proliferate when rare in a population. Because we know from equations (2) and (7) that the success of a group-beneficial trait will depend on the relative size of between-group and within-group variances, we record in Figure 1 both the population frequency of A's and the variance ratio. In this and many identical simulations the group beneficial trait proliferates, in this case as a result of a sustained increase starting around  $t=250$ . The histogram in Figure 1 records the long run behavior of the population – the distribution of values of  $p$  for the 4000 periods following period 200 -- showing, in this case, that  $p$  remains over 0.8 most of the time. (Because we are interested in both the causal relationships among the variables and the long term dynamics of the population, we record both the detailed movements over a 600 period segment of the record of the simulation as well as a histogram of the distribution of the relevant results over a much longer period commencing after 200 periods. In some cases, as in figure 1, the initial conditions are clearly affecting outcomes after 200 periods; but in most cases the effect of the “initially rare” status of both the traits and later the group-level institutions appears to be limited after  $t=200$ ).

Thus once attained, high levels of  $p$  persist over very long time periods. The reason is that as  $p_j$  approaches unity,  $\text{var}(p_{ij})$  approaches zero, bringing within group

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<sup>17</sup> Simulations based on an island model (random migration) produced results similar to the stepping stone model used here (groups are arrayed in a circle and migrants move to neighboring groups.)

updating to a virtual halt for that particular group (if most members of a group are A's then few A's ever meet N's when pairing is random, and so the occasion for updating does not arise.) When this occurs in most groups, the resulting very slow process of updating within groups is then overwhelmed by between-group contests favoring the higher  $p$  groups. The same phenomenon occurs when  $p_j$  is close to zero (as it is at the outset of these runs): with  $\text{var}(p_{ij})$  approximately zero and within group selection consequently minimized, between group pressures predominate giving rise to periodic rises in  $p$ . However these upsurges are easily reversed; the reason is that as  $p_j$  rises towards  $\frac{1}{2}$  in a large number of groups (thus maximizing  $\text{var}(p_{ij})$ ) the force of within group selection against the group-beneficial trait predominates. The proliferation of the group-beneficial trait in the population thus must overcome a "ridge" of heightened adverse within-group selection pressures occupying the mid-range of  $p$ -values.

The evolutionary success of the A-trait in the above simulations is quite sensitive to the parameter values chosen and does not hold for larger groups, higher levels of migration and relatively less frequent intergroup contests. Figure 2 illustrates the constrained parameter space in which  $p$  rises and remains high. Figure 2a shows that for groups of 9 or 10  $p$  attains values over 0.8 most of the time, but for groups of 11 or 12 bearers of the group beneficial trait rarely constitute more than 0.3 of the population. A transparent reason is that with groups of ten or less there frequently occur a good number of all-A groups and these are invincible, converting any group with which they are paired also to all-As (unless the paired group is already all-A). Unless idiosyncratic updating quickly erodes the resulting within group uniformity, the entire population is carried over the ridge to high levels of  $p$ . In many simulations the transition to high levels of  $p$  is immediately preceded by the appearance of a substantial number of all-A groups. The more general reason is that small size greatly increases the between group variance generated by the random fissioning process which occurs when winning groups divide after having assimilated losing populations (or repopulated their sites).

Figure 2b shows that while migration rates of 0.15 and lower yield values of  $p$  of 0.8 or greater most of the time, migration rates of 0.2 yield values of  $p$  which rarely exceed 0.3. Finally in Figure 2c, lowering the frequency of intergroup conflict from  $\delta = .5$  to  $\delta = .4$  alters the dynamic system fundamentally, confining  $p$  to less than .3; raising  $T$  to .6 and further lowering  $\delta$  to .3 confines  $p$  to less than 0.2 almost all of the time.

The remarkably well defined boundaries of the "feasible" parameter space illustrated in these figures is the result of the "ridge" around  $p = \frac{1}{2}$ ; those parameter values which support a movement over the ridge generally sustain very high levels of  $p$  often without a single return to low values of  $p$  in 4000 periods.



The above simulations (and many like them) suggest that with groups of twelve families or more and with per period migration rates of twenty percent or greater the proliferation of an in-group beneficial but individually costly trait occurs with low probability as long as between group contests are not more frequent than within group updating.

### 5. *The co-evolution of individual behaviors and group structures*

We now consider the effect of differences in group social structure on the evolutionary process. We have selected two group level characteristics for the important role they appear to have played in human evolution: social segmentation (positive assortment) and resource sharing. We allow group level institutions to vary a result of both chance and defeat in intergroup conflicts, and study the resulting co-evolutionary process. The first, social segmentation, refers to non-random pairing of individuals within groups (Hamilton (1975), Grafen (1979), Axelrod and Hamilton (1981)). Social segmentation will affect not only the payoffs associated with behaviors, but the process of cultural transmission independently of payoffs. It is likely that in human populations individuals are non-randomly paired to meet both cultural models and others with whom they interact within groups. As a result the probability of meeting a particular type is conditioned on one's own type and may differ significantly from the population frequencies of the traits in question. One might, for example, be disproportionately likely to interact with individuals who have had the same teacher (or the same "parent"), for example, and this would result in non-random pairing in the playing of games. Or the population might be segmented: its members living in communities which are relatively homogeneous culturally or genetically. A "community" is constituted by individuals who interact disproportionately frequently with their one another; it could be a locality or any group more homogeneous than the larger population of which it is a part and within which interaction is more likely than in the population at large. Assortative interactions might also take place in a multi-good economy through strictures governing which types of goods or services one may appropriately exchange with members of ones community as opposed to outsiders. Segmentation does not presume recognition of type, as individuals need not choose the basis on which they are paired.

We formalize the *degree of segmentation* in a way equivalent to the degree of (genetic) relatedness ( $r$ ). Thus if  $\mu_{AN}$  is the probability of an A individual being paired with an N conditional on being an A (with the obvious extensions of this notation to other pairings, and ignoring the group subscript) then:

$$(8) \quad \mu_{AA} = * + (1 - *)p; \mu_{AN} = (1 - *) (1 - p); \mu_{NA} = (1 - *)p; \mu_{NN} = * + (1 - *) (1 - p)$$

then  $\alpha \in [0,1)$  is the "degree of segmentation" and  $\mu_{AA} - \mu_{NA} = \alpha = \mu_{NN} - \mu_{AN}$ . Equation (8) refers only to individual pairing within groups; comparing it with equation (5) it can be seen that segmentation implements *within a group* exactly what between group differences in  $p_j$  accomplish at the population level, namely it creates a difference between A's and N's in the probability of being paired with an A. As a result, the within group difference in the payoffs expected by N's and A's is reduced from  $c$  to  $c - \alpha b$ .<sup>18</sup> Segmentation thus affects differential replication in two ways: it provides advantageous pairings for A's (they are more likely to be paired with fellow A's, and conversely for N's) and it reduces the group average difference in payoffs between the two types, thus lowering the probability that an A will switch type following an interaction with an N.

The second institution we investigate is within-group resource sharing. In some societies – the Ache' in Paraguay, for example – sharing of some kinds of food is so complete that the amounts consumed are unrelated to the amounts collected (Kaplan and Hill, 1985), but we here model a less extreme form of sharing. Suppose some fraction of the resources a family acquires -- perhaps specific kinds of food -- is deposited in a common pool to be shared among all families. This may be modeled as if a linear tax,  $J \in [0,1]$  is imposed on the payoffs resulting from the interactions within a group and the proceeds are distributed equally to all members of the population. The differences in the average payoffs received by N's and A's within a group will now be  $(1-J)(c - \alpha b)$ . Like segmentation, sharing reduces payoff differences; because there is no offsetting effect operating at the group level, resource sharing (as defined here) enhances group selection pressures

Taking account of both segmentation and resource sharing, within group updating is now:

$$(3') \quad \dot{p}_j = - (1 - \alpha) p_j (1 - p_j) T (1 - J) (c - \alpha b) \zeta_j$$

the process of updating being retarded both by the fact that fewer A's now meet N's as indicated by the  $(1 - \alpha)$  term and because when they do meet, A's are less likely to switch (the probability of a switch is now  $(1 - J)(c - \alpha b) \zeta_j$  rather than  $c \zeta_j$ ). Notice that because the positive assortment generated by segmentation both reduces the frequency of interactions with unlikes (the first parenthesis on the right-hand side of (3')) and reduces the mean difference in the payoffs of the two types (the last parenthesis) its

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<sup>18</sup> Of course if  $\alpha > c/b$ , A's will 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. We assume the more challenging case in which  $\alpha < c/b$ , so the A's will only proliferate if group selection pressures are strong enough.

effects are stronger than that of resource sharing (which does only the latter).<sup>19</sup> Using (3'), the stationarity condition for  $p$  becomes:

$$(7') \quad (b-c)' (1-J)(c-^*b) = (1-^*)F(T/6)$$

in which the lefthand side is, as before, the effect of variations in  $p_j$  on group average payoffs relative to the within group difference in payoffs of those bearing the two traits. Equation (7') confirms that both segmentation and resource sharing relax the conditions under which multi-level selection will allow the evolutionary success of a within group beneficial trait.

We turn now to the evolution of the group level institutions described by our parameters  $^*$  and  $J$ . To do this, we extend the process of assimilation/replacement of losing populations and assume that the groups created by the fissioning of the victorious group are governed by the same institutions as the victorious group itself. Essentially the institutions of the winning group are imposed, either on the losing population (in the case of culturally transmitted traits) or on its ecological site (which is repopulated by the winning population in the case of genetically transmitted traits). Because institutions may change not only by imposition but for other reasons as well, we let both  $^*$  and  $J$  evolve for idiosyncratic reasons (with a given probability -- 0.1 in the simulations reported here -- each parameter may adopt a value 0.1 higher or lower than their current value (increases and decreases occurring with equal probability.))

By retarding the rate of selection against the group beneficial trait, both segmentation and resource sharing contribute strongly to group success, as we have seen, and if there were no costs of these social arrangements, we would expect that once  $^*$  and  $J$  are free to evolve, they would increase over time, attaining values of near unity, and bringing within-group selection to a halt. But there are group level costs to both resource sharing and segmentation. By limiting one's partners in joint ventures to ones own community members, segmentation may reduce gains from trade and inhibit individuals from taking advantage of economies of scale. As a result, highly segmented groups will have lower average group benefits (for a given level of  $p_j$ ) than those with a lower value of  $^*$ . We model these costs as a convex function of  $^*$  (the marginal cost of segmentation increasing with  $^*$ ). Like segmentation, the group-selection enhancing effects of leveling institutions may be offset by associated group

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<sup>19</sup> From equation (3') it can be seen that if  $b = 2c$  (the values we have assumed) then variations in  $^*$  have twice the effect of variations in  $J$  in retarding the rate of within group updating when  $^* = 0.25 = J$ . We set the "group costs" of segmentation and resource sharing at  $N^* = 0.5$  and  $N_J = 0.25$ .

level costs. Food sharing, for example reduces the marginal effect of one's own effort on material rewards, and may therefore reduce effort levels and hence average payoffs. As in the case of segmentation we assume that group level costs of leveling are increasing and convex in  $J$ .<sup>20</sup>

We first study the co-evolution of group-level resource sharing and individual level group beneficial behaviors. Notice that while group-level sharing favors the proliferation of the group-beneficial trait, its contribution to the success of the group (by retarding the rate of within group updating against the group beneficial trait) depends on the magnitude of  $p_j(1-p_j)$  (equation (3')). Thus when the A-trait is common, the contribution of sharing to group success will be reduced (because the within group variance of the trait approaches zero as the trait becomes common and so within group updating will be very slow even in the absence of resource sharing.)

The simulation in Figure 3 illustrates this relationship, with an initial upsurge in average levels of resource sharing across the groups initially bootstrapping the frequency of the group beneficial trait to high levels around  $t=225$ , resulting in a decline in resource sharing with the associated substantial decline in  $p$  after  $t=400$  stimulating another upsurge in  $J$ . This process continues over long periods with declines in  $p$  towards  $1/2$  inducing upswings in resource sharing, and conversely. It is evident from the insert that the endogenous evolution of resource sharing has flattened the "ridge" at the mid-values of  $p$ , resulting in  $p$  remaining between 0.3 and 0.8 most of the time. Figure 4 illustrates a similar relationship between  $p$  and  $\alpha$ , with declines in  $p$  creating conditions under which the costs of positive assortment are outweighed by the beneficial effects associated with the retardation of the within group updating process. Levels of assortment of about a third are sufficient to sustain very high frequencies of the A-trait in the long run (recall that for this to occur in the absence of group selection pressures would require much higher levels of assortment, namely  $\alpha > 1/2$ ).

In figure 5 we allow both resource sharing and segmentation to co-evolve with the frequency of the group beneficial trait in a rather unfavorable environment (individual updating twice as frequent as between group conflict, migration rate at 60 percent per generation). The histogram indicates that the group beneficial trait is sustained at levels which are substantial but which occasionally fall below 0.6 and thereby sustain moderately high levels of both resource sharing and segmentation.

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<sup>20</sup> In calculating the winner of an intergroup contest we thus subtract from group average benefits and amount  $N_j J^2$  with  $N_j > 0$ , with an analogous accounting of the costs of segmentation. We have experimented with other formulation of the cost of these group level institutions, with similar results.

From equation (3') we expect resource sharing and segmentation to represent substitutes; by this we mean that the effect of the prevalence of one reduces the marginal group level benefits of the other so that the effect of segmentation in reducing the rate of within group updating is smaller the greater is the degree of resource sharing, and conversely. This expectation is confirmed in the segment of history depicted in figure 5; in response to a decline in  $p$ , resource sharing or segmentation alternately (and rarely together) proliferate among groups, eventually reversing the decline and sustaining high frequencies of the A-trait. This result is rather striking given that it must work against the fact that the group level costs of these institutions are convex in the level of the institutional use, a specification which in the absence of the relationship described above (from equation (3')) would result in the two institutions jointly sustaining moderate levels.

Figure 6 gives the long term frequency of the group-beneficial trait when both segmentation and resource sharing may evolve, under parameter values unfavorable to the evolution of A-trait under the pressure of group selection. By comparison with figure 2, the feasible parameter space is greatly enlarged, now including migration levels as high 0.4 jointly with a rate of within group updating that is three times the frequency of between group contests (the bottom panel). Experiments not shown indicate that group sizes considerably larger than 10 do not preclude the co-evolution of the group beneficial trait and its supporting institutions.

### *6. Conclusion*

We have described a process whereby institutions implementing sharing and segmentation provide an environment within which a group-beneficial trait evolves, and in which these institutions proliferate in the population because of their contribution to the evolutionary success of the group-beneficial trait. Does this model illuminate the process by which human sociality and institutions might have evolved? If we are interested in the evolution of genetically transmitted individual traits, the answer must depend on whether the parameter space in which this co-evolutionary process occurs in our simulations approximates the relevant late Pleistocene environments. We have seen that three parameter values are critical: the first is the relationship of  $T$  to  $\delta$  giving the relative rate of within-group updating compared to between-group conflicts, second, group size, and third, the rate of migration among groups.

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 climate was

exceptionally variable (Boyd and Richerson (1999) 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. In the simulations above we have taken group size to be the number of family units defined as related members who migrate as a unit and remain together when the group divides. Using data from a recent survey of 20<sup>th</sup> century foragers, the average size of nomadic foraging bands is just under seven families, or well within the feasible parameter space for the above simulations.<sup>21</sup>

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 successful groups 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 is likely to contribute to between group variance in ways which our model does not capture. A study of fissioning among Amazonian peoples (Neves, 1995, p. 198) reports that:

The maximum size of a village is constrained by the amount of relatedness or degree of solidarity between individuals [which] springs from three sources: kinship relations, marriage ties, and the influences of political leaders. ...Village fissioning is thus favored by the loosening of kinship ties provided by population growth; and when it happens it keeps close kin together but separates them from more distant kin..the potential line of cleavage is furnished by the division in patrilineages.<sup>22</sup>

As the bearers of the group-beneficial trait are likely to be numerically and socially dominant in the winning group, they may practice what we term *assortative fissioning*, by segregating bearers of the "other" trait insofar as recognition of traits or characteristics correlated with traits allows this. Were this the case much larger group sizes would sustain the evolutionary processes indicated above.

Very little is know about group conflict during early human history (Keeley,

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<sup>21</sup> The average number of people in the 17 nomadic groups reported in Kelly (1995):211 is 28.5, which combined with Kelly's estimate of family unit size gives 6.8 families.

<sup>22</sup> Cagnon (1983):141-3 studied a Yanomamo village that subdivided and found that average relatedness in the prefission village was lower than either of the newly formed units. See also Lizot (1971):39.

1996). But some speculations based on what we know about climate change and likely rates of population growth are possible. Christopher Boehm (1999):19 writes:

In very rich stable environments it makes sense that prehistoric population densities rose, that increasingly proximate and numerous bands began to compete for resources, and that eventually this would have made for lethal political trouble even if resources originally had been more than adequate. ... These varying conflict patterns would have periodically increased the force of natural selection operating at the between group level as some bands were decimated while others flourished and eventually had to fission. [In response to dramatic oscillations in climate in the last Pleistocene interglacial period] foraging bands were obliged to make major adjustments quite frequently, and surely these often included bands adjusting to neighboring bands as well as bands adjusting to changing biomes.

His conclusion is that

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

Carol 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 percent of the groups had warfare every two years or more frequently. Even excluding those groups who either had horses or relied on fishing, warfare is described as “rare” in only 12 per cent of the groups.

We have interpreted the updating process (whether genetic or cultural) as taking place once a generation (although cultural updating could be much more frequent). Our simulations have assumed that decisive group conflicts occur anywhere from twice a generation ( $T=.5$ ,  $6=.5$ ) to once every fourth generation ( $T/6 = 4$ ). Many of the conflicts reported in Ember are not decisive in the sense used here (imposing cultural assimilation or fitness costs on the loser); but even taking this into account it seems that our feasible parameter space could capture some of the relevant early human environments. Moreover if individually costly but group beneficial traits did evolve by the process modeled here—by imposing costs on outgroup members – it seems likely that their proliferation would have contributed to the frequency of lethal and other serious group conflicts.

While movement between ethno-linguistic units was probably quite rare, it seems likely that substantial rates of migration among the bands making up these units occurred. On the basis of contemporary evidence, however it seems unlikely that migration rates would exceed eighty percent a generation ( $m=0.4$ ), a level which (as figure 6 shows) does not preclude the evolution of the group beneficial trait.<sup>23</sup>

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 figures 3 to 6.

Other aspects of human social structure may, however, limit the range of evolutionary phenomena to which the classical group selection model applies. The evolution of general rules of appropriate social behavior and the concomitant development of collective enforcement of moral standards through legal sanctions, collective monitoring and punishment or shunning of transgressors by peers, indoctrination, and other means may attenuate or even eliminate within group individual selection against socially beneficial but individually costly behaviors.<sup>24</sup> Property rights enforced by third parties and the large scale provision of public goods are recent examples of this process. Where this happens, it does not diminish the importance of group selection, but rather enhances it, because within group selection pressures are thereby weakened. But when groups are able to protect group-beneficial behaviors from exploitation, the puzzle which group selection was initially introduced to resolve disappears, for the evolution of individually costly but socially beneficial behaviors is then explained simply by the greater net cost of other less socially beneficial behaviors.

Of course the ability of human groups to impose sufficient costs on norm violators to protect group-beneficial behaviors is imperfect. This is true both because the behaviors in question are often not readily subject to detection and punishment and because the capacity to impose collective legal and other sanctions within groups is often captured by those whose interests may compete with the objective of protecting group-beneficial behaviors.

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<sup>23</sup> Migration rates for the thirteen societies surveyed by Rogers (1990) averaged twenty-two 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.

<sup>24</sup> Boehm (1982) and Campbell (1985) are early statements of this view. See also Alexander (1987).



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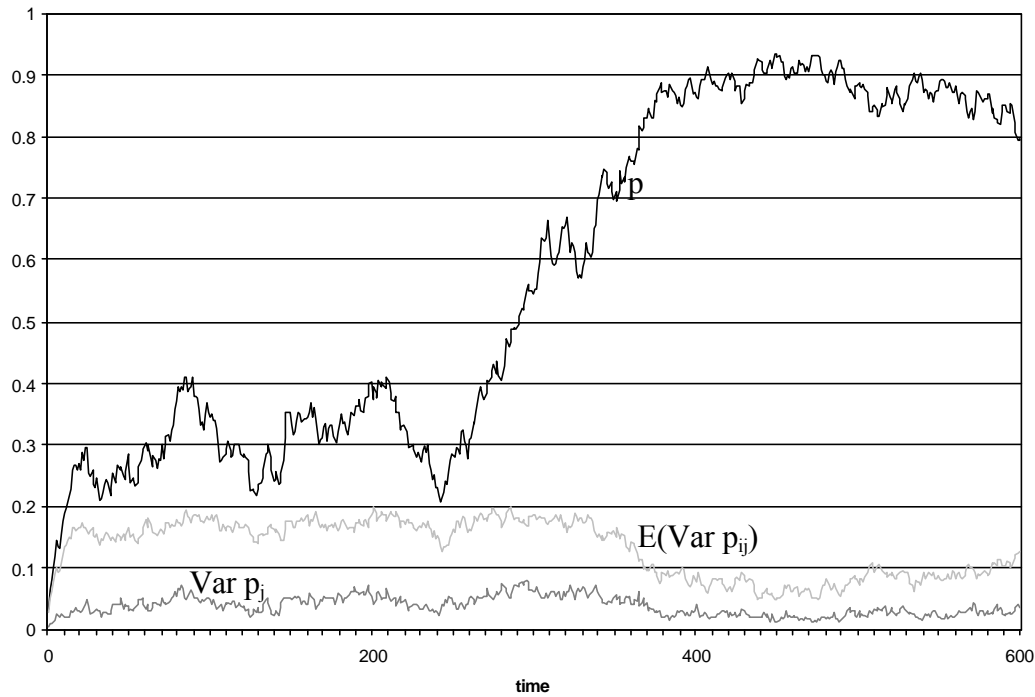


Figure 1a. Proliferation of an Initially Rare Group-Beneficial Trait without Resource Sharing or Segmentation but Otherwise Favorable Conditions (with Between and Within Group Variances  $n=10$ ;  $T=0.5$ ;  $\delta = 0.5$ ;  $m=0.15$ )

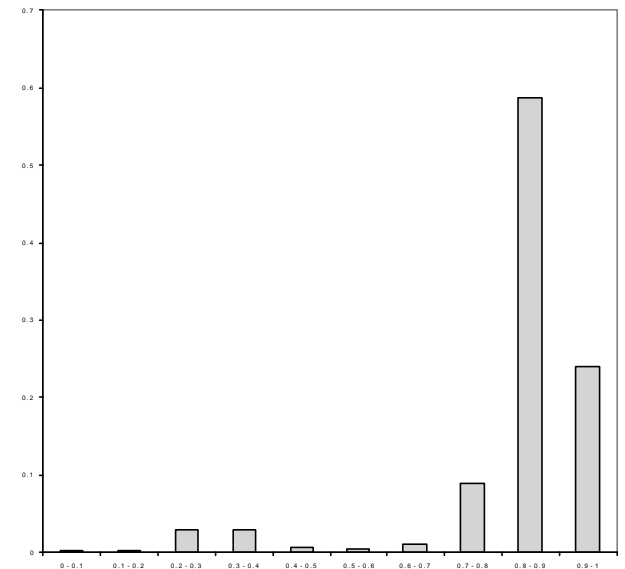


Figure 1b. Long Term Evolutionary Success of a Group Beneficial Trait: Distribution of  $p$  over 4000 periods beginning with  $t=200$ .

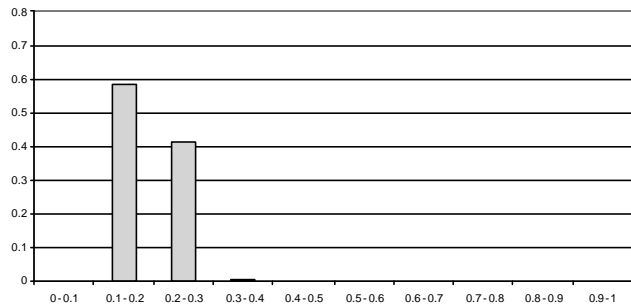
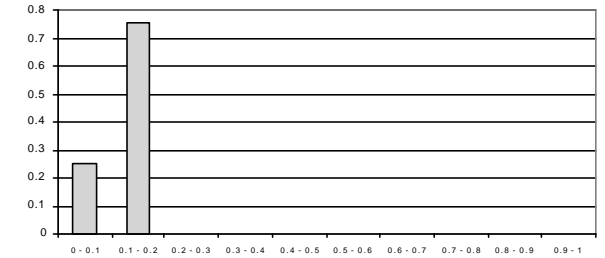
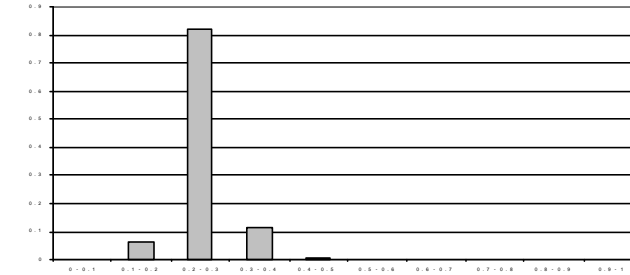
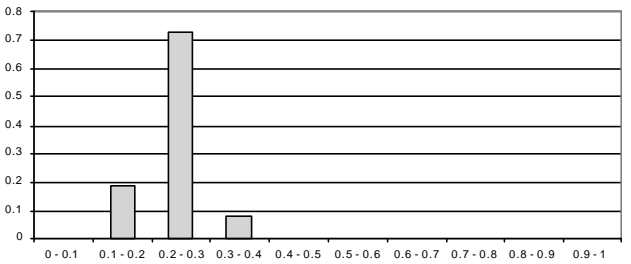
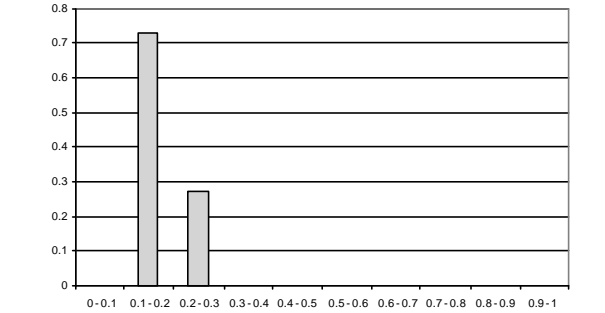
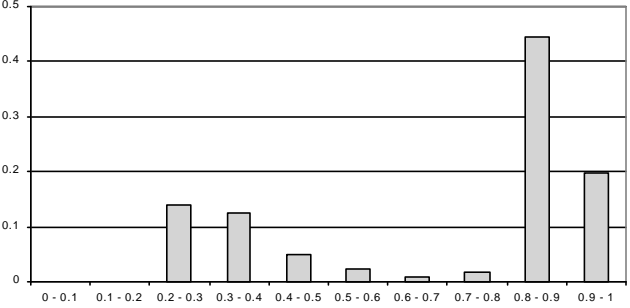
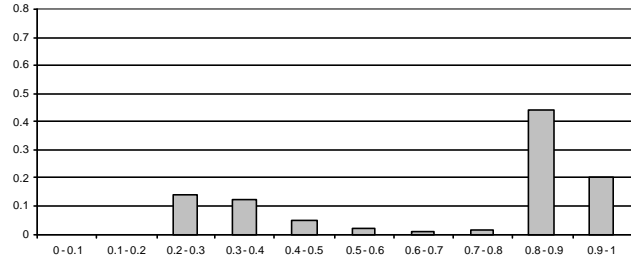
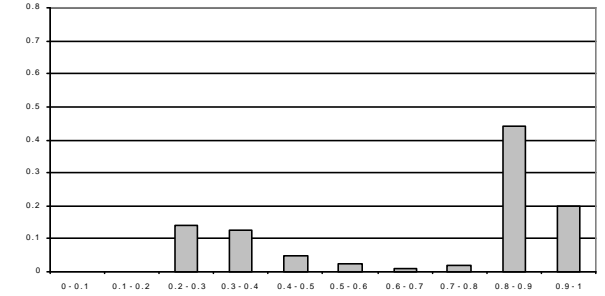
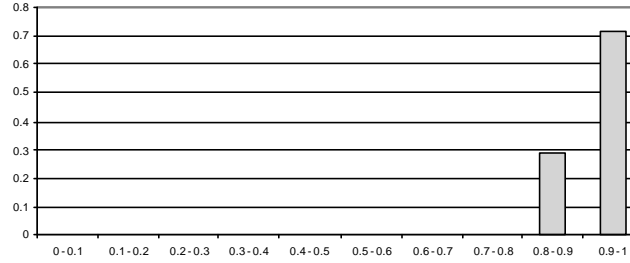
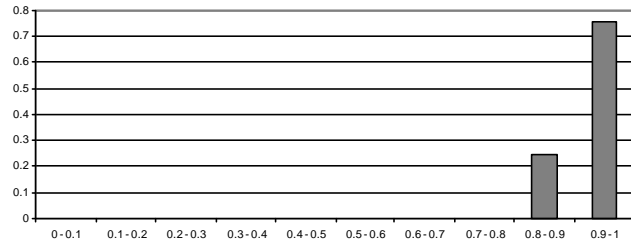


Figure 2a: Distribution of  $p$  over 4000 periods: Effect of group size. The panels show runs with groups of size 9 to 12 from top to bottom.

Figure 2b: Distribution of  $p$  over 4000 periods: Effects of rates of migration from top to bottom  $m = 0.10$ ,  $m = 0.15$  and  $m = 0.20$

Figure 2c. Distribution of  $p$  over 4000 periods: Effects of the frequency of individual updating and group conflicts. The values of  $T$  and  $\delta$  respectively are, for the top panel  $T = 0.5$ ,  $\delta = 0.5$ ; middle panel  $0.5$ ,  $0.4$ , bottom panel  $0.6$ ,  $0.3$ .

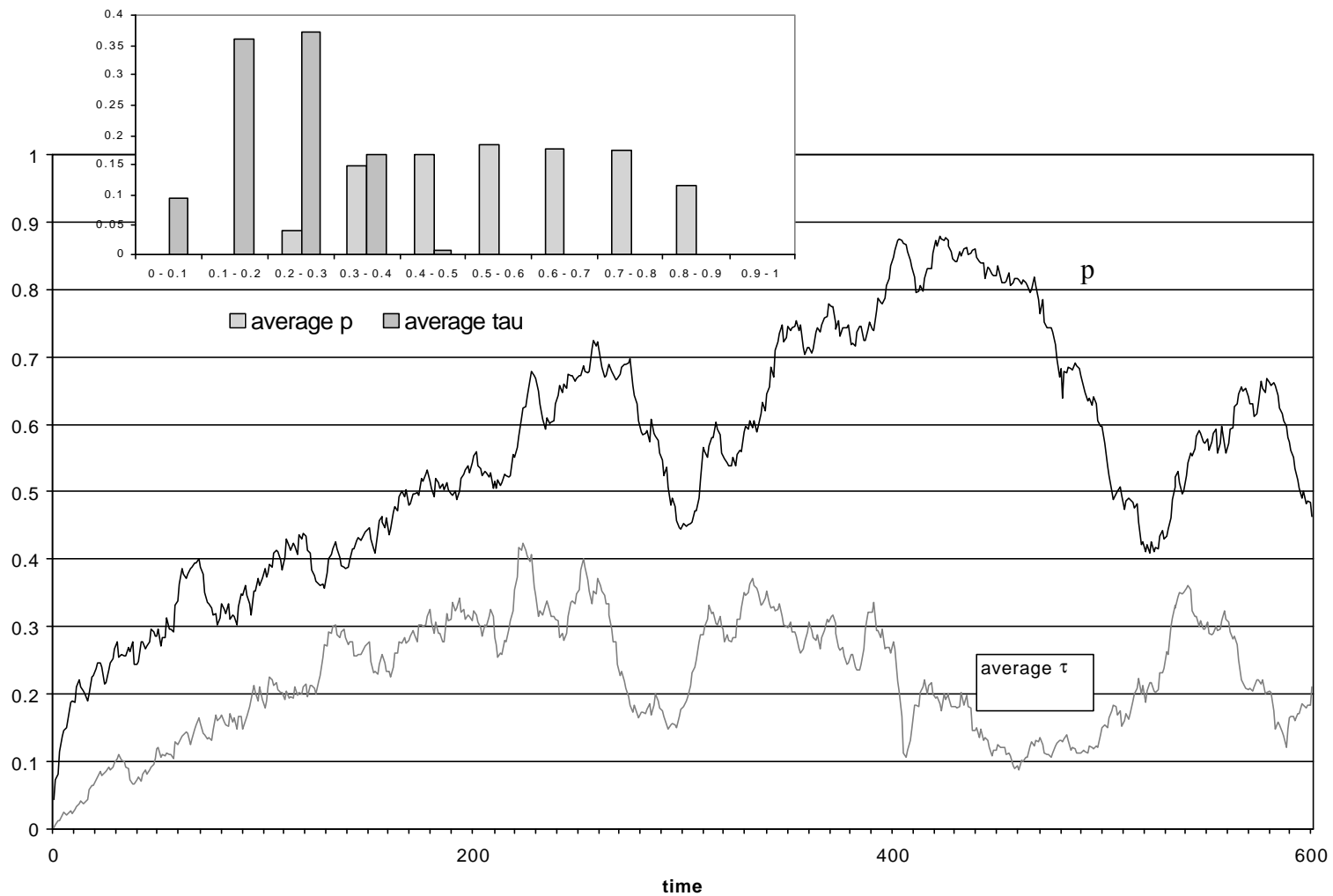


Figure 3 Co-evolution of Resource Sharing ( $J$ ) and a Group Beneficial Trait ( $p$ ) Under Unfavorable Conditions, when both are initially rare. Parameter values ( $n=10$ ,  $T=0.5$ ,  $\beta=0.5$ ,  $m=0.3$ ) The insert panel shows the average values of  $p$  and  $J$  over 4000 periods beginning with period 200.



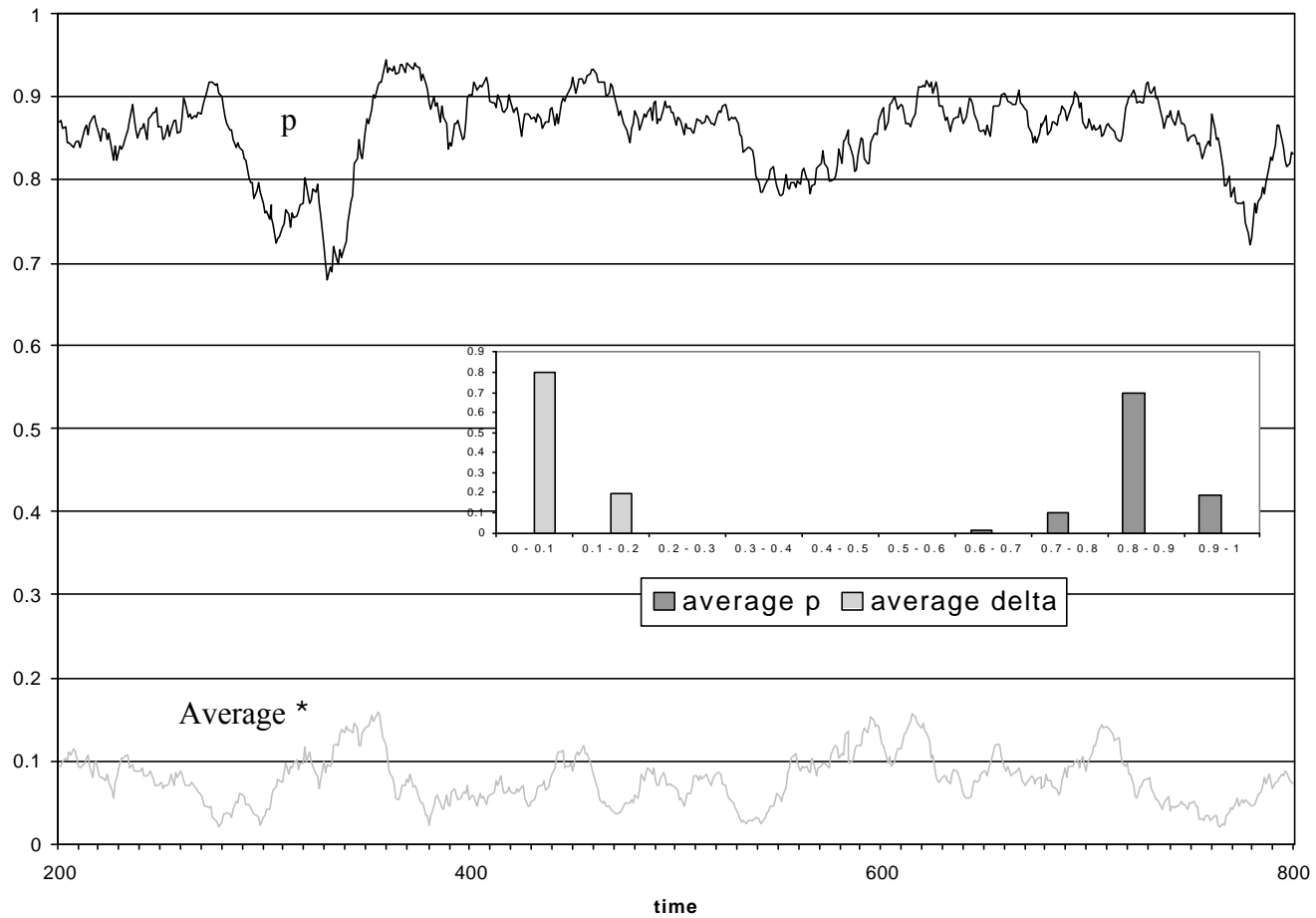


Figure 4. Co-evolution of Segmentation (\*) and the Group-beneficial individual trait (p) under unfavorable conditions (same parameter values as Figure 3). The insert panel shows the average values of p and \* over 4000 periods beginning with t=200.

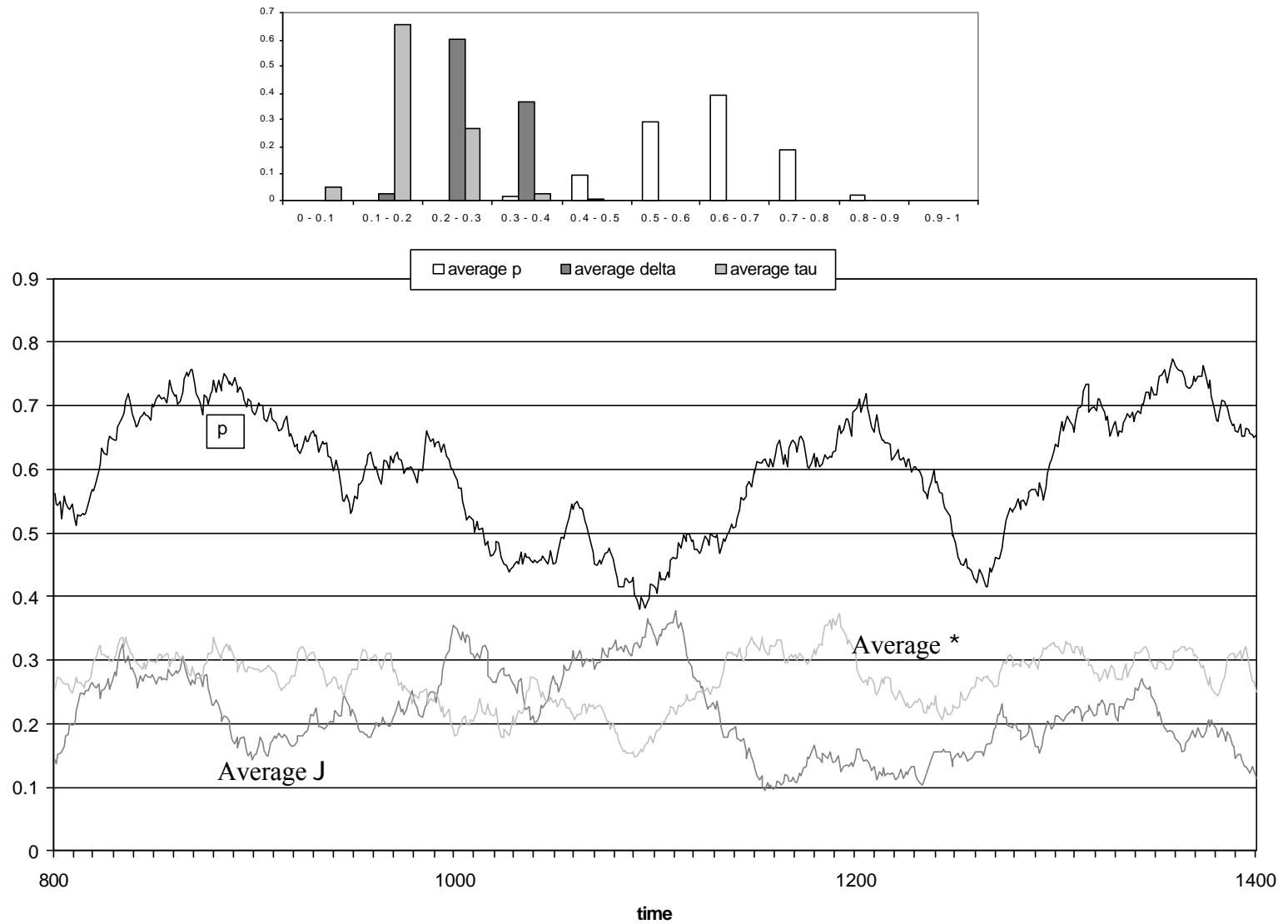


Figure 5. Co-evolution of Resource Sharing, Segmentation, and a Group Beneficial Trait Under Unfavorable Conditions (same parameter values as figure 3 except that  $T = 0.6$  and  $\delta = 0.3$ ). The insert shows the average levels of  $J$ ,  $*$  and  $p$  over 4000 periods beginning with  $t=200$ .

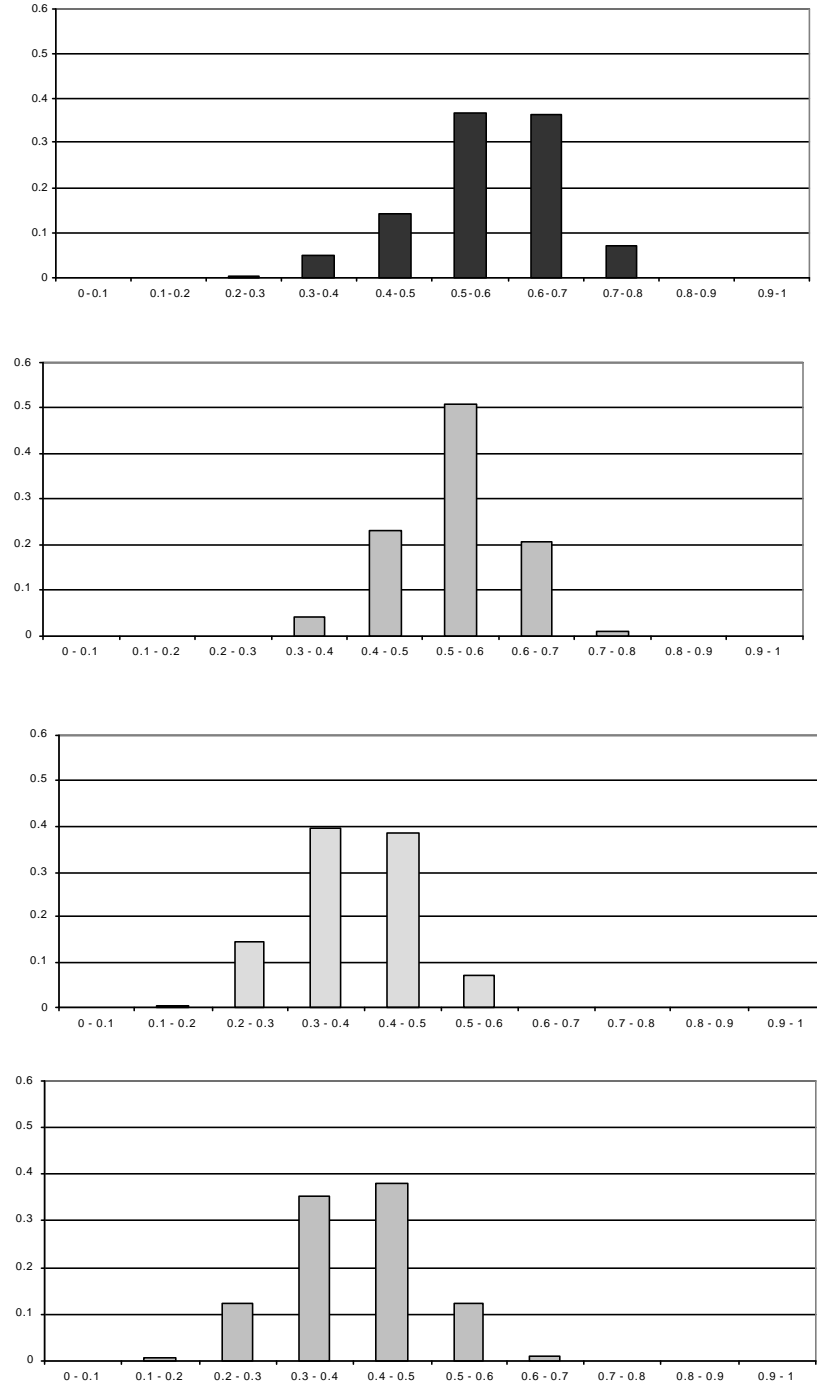


Figure 6. Frequency of the Group-Beneficial Trait with Endogenous Resource Sharing and Segmentation (Distribution of  $p$  over 4000 periods beginning with  $t=200$ , for groups of size 10 and: top panel,  $T=0.6, \beta=0.3, m=0.4$ ; second panel,  $T=0.75, \beta=0.25, m=0.3$ ; third panel,  $T=0.8, \beta=0.2, m=0.3$ ; bottom panel,  $T=0.75, \beta=0.25, m=0.4$ .)