THE NATURAL SELECTION OF ALTRUISTIC TRAITS

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Proponents of the standard evolutionary biology paradigm explain human "altruism" in terms of either nepotism or strict reciprocity. On that basis our underlying nature is reduced to a function of inclusive fitness: human nature has to be totally selfish or nepotistic. Proposed here are three possible paths to giving costly aid to nonrelatives, paths that are controversial because they involve assumed pleiotropic effects or group selection. One path is pleiotropic subsidies that help to extend nepotistic helping behavior from close family to nonrelatives. Another is "warfare"—if and only if warfare recurred in the Paleolithic. The third and most plausible hypothesis is based on the morally based egalitarian syndrome of prehistoric hunter-gatherers, which reduced phenotypic variation at the within-group level, increased it at the between-group level, and drastically curtailed the advantages of free riders. In an analysis consistent with the fundamental tenets of evolutionary biology, these three paths are evaluated as explanations for the evolutionary development of a rather complicated human social nature.

KEY WORDS: **Altruism; Cooperation; Egalitarianism; Group selection; Pleiotropy; Warfare.**

An "altruistic gene" is defined as any gene that is positively selected by natural selection taking place *between* groups, but negatively selected by natural selection *within* groups.[1] Since the early 1970s, the selection para-

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dox of "altruism" (Haldane 1932) has preoccupied a rapidly expanding community of scholars, and (until recently) the conservative conclusion was all but unanimous. Natural selection can directly support innately prepared generosity only if such help is directed either at close kin (Hamilton 1964; Williams 1966; see also Trivers 1972) or at partners with whom strictly equalized reciprocation prevails over time (Trivers 1971). These conclusions stem from the parsimonious paradigm promulgated by R. D. Alexander (1974) and E. O. Wilson (1975), which made evolutionary sense of social species from ants to wild dogs but denied any realistic possibilities for group-selected altruism in mammals. Wilson's (1978) further discussion of "soft-core altruism" and Alexander's (1987) argument that human networks of indirect reciprocity might be sustainable by inclusive fitness provided an adaptation-oriented body of theory, one applied to human social life in thousands of publications.

This standard sociobiological paradigm holds that natural selection can support only innate behaviors that are individually selfish or nepotistic, that is, behaviors that are the product of within-group selection. It follows logically that human nature, itself, must be ultimately selfish and nepotistic. However, after being fashionable for three decades this supposition continues to pose perplexing problems, both scientific and philosophical. Indeed, in the wake of earlier attempts by Wilson (1978), Alexander and Borgia (1978), and Alexander (1987) to reconcile what we intuitively understand about the altruistic side of morality with the formal dictates of social biology, there have been continuing efforts (e.g., J. Q. Wilson 1993; Wright 1994; Ridley 1996) to explain satisfactorily, in terms of selfish nepotism, the behavior of a species which by common sense certainly *appears* to exhibit some innate altruism. The empirical problem is that generously inclined humans do sometimes make reproductively costly contributions to the success of nonrelatives, contributions that apparently are uncoerced, lack precise reciprocation, and might most readily be explained by group selection.

Darwin (1871) was the first to suggest that with groups serving as vehicles of selection, natural selection might directly support innate generosity toward non-kin. More recently, as a pioneer in evolutionary psychology, Donald T. Campbell (1965a, 1972, 1975; see also Campbell and Gatewood 1994) has helped to probe the puzzle of human ultrasociality (see also Boyd and Richerson 1991, 1992). In terms of useful mathematical modeling, a "multilevel" natural selection theme has been emphasized by biologist D. S. Wilson (e.g., 1975, 1977, 1980, 1983, 1989, 1992, 1997; see also Wade 1978), the most comprehensive general arguments being set forth in Wilson and Sober 1994 and Sober and Wilson 1998. And in a variety of anthropological contexts (e.g., Boehm 1978, 1982, 1986, 1996, 1997a, 1997b, 1999a, 1999b), I have suggested that genetic group-selection explanations could be particularly applicable to egalitarian humans who make consensual decisions and curtail free riding—an argument continued here. However, for three decades the received wisdom for *all* social mammals has been that selection taking place between groups is simply too feeble, mechanically, to support altruistic traits (see Alexander 1974; Williams 1966; E. O. Wilson 1975).

The problem poses difficulties even in its definition. Introspection and observation of life around oneself would indicate that, quite often, human acts deemed to be broadly "altruistic" (1) are merely socially enforced and therefore dissembled, (2) are strictly limited to helping kin, (3) are limited to reciprocal donations that are equalized over time, or (4) are tied to selfish impulses to gain recognition, praise, or other rewards. Sociobiology supports such intuitions (see Alexander 1987; Ridley 1996; Trivers 1971, 1972; Wilson 1978; Wright 1994). However, in addition I am suggesting that (5) we may sometimes experience impulses involving "spontaneous generosity," as it were, that has little to do motivationally with any of the above—and entails helping group members who are neither kin, nor partners in strict reciprocation.

Because so much of the generous behavior in human life would appear to mix two or more of these five factors, the resulting motivational "muddiness" makes it relatively easy to stick with an elegant standard paradigm that essentially denies any significant altruism to human nature. But this influential and powerful means of explanation has remained counterintuitive for our own species. Some theories are powerful precisely because they do not accord with common sense, but in this instance there remain three major problems (see Boehm 1999b).

The first is to explain innately generous behaviors of the type that are regularly mentioned as counter examples: firemen rushing into burning buildings, and so on. In considering such behaviors, ones that seem to be motivationally removed from selfish imperatives, our methods need not be limited to Cartesian introspection or personal impressions. On the world's various continents, ethnographers report that people not only cooperate extensively with non-kin on a *generalized* basis, but sometimes one-sidedly assist nonrelatives within their groups, and sometimes even help total strangers. It can be argued, of course, that such "reproductively suicidal" actions are merely the effect of prosocial socialization (e.g., Goody 1991; see also D. S. Wilson 1983), or an effect of adult human tendencies to social conformity (see Boyd and Richerson 1985; Campbell 1975; Simon 1990; Waddington 1960), or even that individuals are merely being coerced by punitive groups (Boyd and Richerson 1992).

But this is where the second problem arises. Why do humans universally arrive at socialization techniques and moral codes that not only condemn and very effectively punish a variety of selfish behaviors by means of aggressive sanctioning, but also very actively promote cooperation and altruism (e.g., Campbell 1972, 1975; see also Boehm 1999b; Hinde and Groebel 1991; Sober and Wilson 1998; Wilson and Kniffen, this issue) on a highly *positive*, prosocial basis? This positive side of morality has been substantially under-perceived and under-reported by ethnographers, one reason being that the sheer drama of ridicule, ostracism, expulsion, and execution naturally captures our attention and the attention of people we study. As a result, reports on moral codes usually make nonliterate cultures seem far more specific and forceful in proscribing than in prescribing. As a social theorist, Barnsley (1972:54–55) considered this issue, saying that one

> basic attribute of values and norms is that they may be positively or negatively accented. . . . Sociologists and ethnographers have frequently either argued or assumed that rules are normally most explicit about what is bad; the good is then residual.

Barnsley thought that this inadvertent neglect might stem from the fact that we are used to modern law, which is basically proscription-oriented.

For whatever reason, in sociology (e.g., Black 1984) and anthropology (e.g., Freilich et al. 1991), recent general theories of social control continue to be cast mainly in terms of antisocial deviance, prohibitions, and punishment, rather than emphasizing prescriptions and use of praise. However, when ethnographers investigate norms rather than acts of social control, or broadly evaluate nonliterate societies as to their prosociality (see Sober and Wilson 1998), the positive side of moralistic manipulation by groups does become prominent. In a substantial survey of egalitarian societies (Boehm 1993, 1999b), I searched impartially for value statements about band or tribal political leaders and was surprised to see that the prescriptive and proscriptive aspects of the ethos were about equally emphasized when role expectations were reported. In fact, "generosity" was mentioned far more frequently than "stinginess." But generally the relatively subtle, positive side of social manipulation by groups receives less explicit attention than the negative, and therefore tends to stay out of focus.

In terms of social biology, it is easy to understand why law-abiding selfish nepotists would band together aggressively to create moral systems that are *negatively* oriented, combining proscriptions and punitive sanctions to assertively protect themselves and their familial interests against other selfish nepotists who are deviant. Self-defensive suppression of deviance is undertaken aggressively in all human communities, and this accords with a tough-minded, sociobiological view of human nature—an essentially selfish nature that permits the formation of large, aggressive, moralistic coalitions composed of self-interested individuals who are prepared to engage in punitive sanctioning. The biological puzzle concerns the positively oriented side of human social blueprints, which espouse altruistic attitudes and prosocial acts that benefit unrelated group members who cannot reciprocate. The underlying basis for such attitudes and behaviors is not readily explained in terms of egoistic or nepotistic self-interest.

The third problem is that often humans exhibit a tendency to conform spontaneously to local prosocial norms—without having to be threatened or punished. For example, among many mobile hunter-gatherers the most able hunters willingly acquire game for the entire group, and this meat is widely distributed with a minimum of bickering even though unrelated families are sharing it. Such routines stay in place because bands emphasize generosity, and in most cases there appears to be enough prosociality in human nature to make the person who is expected to be generous willingly responsive. If we were innately driven to be selfish nepotists and nothing more, it is dubious that these prosocial blueprints would be working very well.

The effects of positive and negative sanctioning are difficult to disentangle. But my point will be appreciated by any anthropologist who has conducted extensive field work with people who get along reasonably well. Human beings living in moral communities are motivated by desire for esteem as well as by fear of punishment, and most of them seem to have identified heavily with the prosocial side of their own moral system (see Piers and Singer 1971). For example, Kelly (1995) cites a hunter-gatherer study in which Leacock's informant, a Mistassini Cree, makes it clear that not to share with someone who was hungry would violate a norm that was well-internalized (see Leacock 1969).

The three questions I have raised about human prosociality require an answer. One explanation might be that positive codes are merely being held in place automatically by powerful, blindly operating *cultural* processes (e.g., Boyd and Richerson 1985; Campbell 1965b, 1975; see also Wilson and Kniffen, this issue), and that evidence favoring a strongly prosocial side to human nature is illusory. Another might be that human cognitive sophistication helps to do the job. For example, a morally united group of aggressive, nepotistically selfish individuals somehow decides that pleas for generalized generosity to other group members may serve their selfish interests over the long term, because such pleas help to define selfish deviance. Such answers are consistent with rather complicated social-biological theories of human social behavior which try to explain away generous behaviors in terms of (inclusive) genetic self-interest or strict reciprocity and bring in cultural factors such as public opinion or social control as convenient helpers. But such approaches fail to tackle the underlying basis of prosociality as seen in hunting bands.

As Richerson and Boyd (this issue) characterize them, complex societies are at the same time coercive and voluntaristic. The same is true of nomadic foragers, whose *willing* cooperation takes place mostly among kinsmen but very significantly among nonrelatives. We need to know more about the ultimate basis for this voluntaristic side of hunter-gatherer band life, and my general hypothesis will have to do with our immediate ancestors. I shall propose that they were preponderantly selfish and nepotistic, but there was also a significant element of innate altruism in their genetic makeup that helped to create significant *ambivalences* at the level of psychological motivation (e.g., Campbell 1965a; Campbell and Gatewood 1994; see also Boehm 1989, 1999b; Erdal and Whiten 1994; Knauft 1994; Masters 1989; Sober and Wilson 1998). One innately structured type of social ambivalence is that which pits individualistic selfishness against nepotism; people can be caught between their own needs and those of close family members. But the focus will be on the tension between traits that make for selfish nepotism and those that extend helpful generosity to other group members who are nonrelatives. If band members are disposed to assist non-kin in the band, this is likely to require a group selection argument.

This type of ambivalence provides the motivational wherewithal for humans to invent and maintain the two-sided moral codes discussed above, which promote not only familial interests but group interests. In advancing the argument that humans are at least moderately disposed to help individual nonrelatives or donate reproductive effort to their entire groups, and that therefore they are susceptible to prosocial manipulation by the group, one faces a specific and formidable problem. In terms of selection mechanics, how could such a significant altruistic component have evolved in human nature?

THREE HYPOTHESES

At the outset, I distinguish the evolutionary logic I am using from that of the mathematically naive "group selectionists" who were read out of evolutionary biology in the 1960s. I will not be suggesting that this substantially prosocial side of moral life itself can be counted as compelling "functional" evidence that natural selection must be supporting altruistic traits in our species—even though important questions are raised by its prominence. Rather, to explore the possibility that altruistic traits could have been maintained in Paleolithic human gene pools I shall be further developing a specific hypothesis about selection mechanics. My suggestion is that a "political revolution," experienced by Paleolithic humans, created social conditions under which group selection could robustly support genes that were altruistic (Boehm 1997a, 1997b).

This main hypothesis is based on the hunter-gatherer's "egalitarian syndrome" (Boehm 1999b; Knauft 1991; Woodburn 1982), which refers to typical political and social features of extant nomadic foraging life. Human bands surely have been moral communities for a very long time, and I believe that their egalitarian ethos, with its pervasive effects on social and political life, affected the selection of altruistic traits in three ways. Typical nomadic band life reduced phenotypic variation *within* groups; it amplified phenotypic variation *between* groups; and, very important, through moralistic sanctioning it worked robustly to suppress the reproductive advantages of free riders. As a result, three factors that block the retention of altruistic genes were substantially modified after humans became moral and egalitarian. This main hypothesis is, indeed, a "group selection" argument, but normally it is extinction rates that are the focus in arguments about levels of selection. Here, it will be *variation*.

Before I proceed to this main hypothesis, I shall treat two others rather briefly. First, I have a preliminary hypothesis that involves what might be called "pleiotropic subsidies" and does not require group selection. There is a second preliminary hypothesis, that prehistoric warfare might have contributed to retention of altruistic traits by raising extinction rates at the between-group level. I shall rather quickly consider these possibilities before I go on to the hypothesis about egalitarianism.

HYPOTHESIS I: "PLEIOTROPIC" SUBSIDIES

When people sacrificially assist distant kin or non-kin, such behavior just *might* be a reproductively costly side-effect of powerful nepotism. I have in mind social behaviors that are so well supported by inclusive fitness that they could be extended, at a moderate cost, to non-kin as a "side-effect" that somehow defies natural selection. The modeling assumption is that the same genes are preparing both assistance to kin and assistance to non-kin, and that somehow natural selection cannot isolate the individually maladaptive side-effects and winnow them out. This could be because precisely the same genes are doing two different jobs—one very useful to inclusive fitness but one merely useful to the group (e.g., Boehm 1981; Simon 1990).

Technically, a pleiotropic gene is one that has two (or more) distinct phenotypic manifestations or functions. Pleiotropy has been invoked to explain the evolution of senescence as discussed by Alexander (1987), but with respect to the problem of altruism it has rarely received explicit attention because evolutionary biologists make the simplifying modeling assumption that one gene prepares just one behavior trait (Boehm 1979). This automatically rules out a type of explanation that could help to account for certain kinds of reproductively generous human behavior such as third-party conflict management (Boehm 1981), or other types of human altruism that are promoted by group mores (Simon 1990), or apparently "indiscriminate" extensions of nepotism that are found in certain other species (e.g., Eibl-Eibesfeldt 1978, 1989, 1996; Goodall 1986).

Classical pleiotropy involves a single gene that produces both a morphological effect and a behavior, or two distinctly different instances of either. I shall take some liberties in suggesting that such explanations could be extended to include a gene that prepares two very similar behaviors that have distinctly different consequences in terms of levels of selection. Thus, a nepotistic behavior like conflict management within the family or nurturing one's own children, behaviors that are very profitable to inclusive fitness, might be extended "pleiotropically" to non-kin and still be retained in gene pools. This could be the case even in the absence of group selection, so long as the overall benefits of such genes significantly outweigh their costs.

The empirical assertion that humans extend nurturant behaviors to unrelated group members is far from new. Citing Aristotle, James Q. Wilson (1993) suggests that sentiments of sympathy involved with the parent-child relationship generalize to society as a whole. There is no precise explanation, however, for how the reproductive effort involved in this transfer of helpful behavior from offspring to genetic strangers could be sustained by natural selection. Eibl-Eibesfeldt (1978:101) quotes Darwin who, obviously unaware of pleiotropic genes, discussed the ways in which humans express their prosocial instincts beyond the confines of kinship, and he also cites Gehlen (1969), who holds that the ethos of altruism derives from the extended family but generalizes to non-kin. In his own work he focuses on "group-uniting mechanisms," proposing that both birds and mammals have arrived at patterns of caretaking for the young which generalize to adults, and result in mutual aid and altruistic groups; he pinpoints the mother-child relationship as the locus of such behavior in higher social species (Eibl-Eibesfeldt 1978:244–245, 1989). Elsewhere, he sums up his more recent arguments:

> With the evolution of nurturant motivations and behaviors a set of "preadaptations" for adult bonding came into being. These included family defense, the ability for individual recognition and bonding, and neonate signals triggering nurturant responses and the motivation to seek nurturance. . . . In human beings the small-group ethos of face-to-face-communities is basically nurturant (Eibl-Eibesfeldt 1996:779).

It is interesting that Eibl-Eibesfeldt places "preadaptations" in quotes; this suggests that it might be difficult to specify the selection mechanisms when people move beyond nepotism. Obviously, there is a difference between a useful preadaptation that continues to be positively selected in a new environmental context and an individually deleterious behavior that somehow stays in place in spite of its reproductive costs.

There are many types of human nepotism, in the form of nurturance, protection, and generous cooperation, that can be extended from kin to non-kin. They reach as far as ultimate patriotic self-sacrifices to protect the group, which for humans are very difficult to explain just on the basis of kin selection or reciprocal altruism (see Campbell 1975). There is also occasional adoption by non-kin of children carrying the genes of genetic competitors, which occurs with varying frequency in different culture areas (see Silk 1990). But while other primates also invest in unrelated orphans (e.g., Goodall 1986), intensive, high-risk warfare seems to be ours alone (Boehm 1992).

If we consider proximate causation among hunter-gatherers, many of the mores that favor generosity to all band members are very similar to the norms that apply within families. The fact that humans selectively apply kin terms to nonrelatives (see Fox 1989), and sometimes bond strongly with them, may be the phenotypic obstacle that natural selection has encountered in trying to eliminate these individually maladaptive side-effects (see Boehm 1999b). But if this "pleiotropic subsidy" hypothesis has any merit, it applies only to altruistic behaviors that are very similar to nepotistic ones. It is not a general theory of altruism, it does not require altruistic genes as defined above, and it definitely requires more work.

HYPOTHESIS II: PALEOLITHIC WARFARE

It has been argued that altruistic genes could be selected straightforwardly and robustly if between-group extinction rates reached parity with within-group extinction rates, and that intensive warfare might be an agency for such selection (Alexander 1971, 1974; Alexander and Tinkle 1968; Frank 1988; E. O. Wilson 1975; see also Bigelow 1969; Eibl-Eibesfeldt 1982; Pitt 1978). There are two jokers in the pack. One is the very significant differences between individuals and groups, as macro-units of selection that exhibit variation and are subject to extinction. Individual life spans in the Paleolithic were finite and relatively short, while for hunting bands "life spans" obviously are difficult to estimate but were likely to be far greater than about 35 years. Thus, without truly *intensive* warfare, the extinction rates for groups would be far, far lower. The other joker is that so little can be determined reliably about patterns of group conflict before the Mesolithic (Keeley 1996).

Better documented are Post-Pleistocene human horticultural populations that are tribal, tend to fight a lot, and may nearly wipe each other out rather frequently if they face high population density and limited resources (see Soltis et al. 1995). But it is suggested that even these high group-extinction rates would support nothing more than *cultural* group selection, which operates quite differently from genetic group selection.[2] Keep in mind that with gene selection, because of free riders group extinction rates must essentially become comparable to individual extinction rates if altruistic genes are to be supported at socially significant levels, and that it also helps if groups are relatively small. Furthermore, conditions of migration and dispersal for propagation of new groups must be met (see Wade 1978). A basic requirement, of course, is that for group selection to support altruism some propagules must contain more altruists than others (see Wilson and Kniffen, this issue). With respect to all of these issues, archaeological data provide few direct clues except as to the sizes of bands, which would appear to have been suitably small. However, the abundant behavioral data from extant foragers, and relevant data about later Pleistocene climates, make possible the formation of some tentative general hypotheses in this area.

First, let us consider group selection theory. The kinds of groups I have in mind are multifamily hunting bands of the type that predominate today (Kelly 1995): some of the families will be closely related, some distantly related, and some unrelated. Unless pleiotropic subsidies are operative, group selection is needed to account for any reproductively generous behavior among the unrelated families. By contrast, generosity among family members or closely related kin is readily accounted for in terms of nepotism, which is supported by within-group selection.[3]

Selection between human groups can proceed similarly to selection among individuals (E. O. Wilson 1975; Sober and Wilson 1998), and, as with individuals, the selection process can be indirect, or quite direct and bloody. At the indirect level, if nearby bands significantly vary in their adaptive strategies, then differences of skill, or luck, or degree of cooperation can affect the growth or decline of these larger units of selection—just as individual reproductive success is affected by variations in individual adaptive strategies. Individuals also compete *directly* for resources, as with certain types of sexual selection or social dominance hierarchies in which individual dominance brings advantages of feeding as well as mating (Ellis 1995), and there also can be direct competition between *groups*. For example, extant bands go on revenge or raiding expeditions (see Ember 1978), or stand together to deter outsiders from using their resources by social or military means (see Kelly 1995).

The very effective hunting weapons available in the Upper Paleolithic would have amplified the homicidal consequences of both individual and group conflicts, and they may also have led to loss of both abundant body hair and highly ritualized intimidation displays as humans became anatomically modern (Boehm 1999b). However, we face a daunting empirical question: how behaviorally similar were Paleolithic hunter-gatherers to their extant counterparts, and were they actually likely to conflict as bands? Most anthropologists (e.g., Kelly 1995) take a negative tack in considering extant foragers as models, and many of their concerns are well-justified. However, I believe that certain similarities and differences can be sorted out if one considers the full range of hunter-gatherer adaptations in the context of local ecology, and then compares modern environments with far more changeable ones of the later Pleistocene.

Let us begin with behavioral potential. Extant foragers exhibit a wide spectrum of subsistence strategies and social arrangements (see Kelly 1995), and surely Upper Paleolithic hunter-gatherers were just as variable: they were the same species, and to say their environments were as variable as present ones is a serious understatement (see Potts 1996, 1998). Moreover, archaeological and other evidence points to their living similarly in multifamily bands that were smallish (Dunbar 1996; Mithen 1990), and it is extremely likely that they were politically egalitarian (Boehm 1982, 1997b, 1999b; Knauft 1991, 1994; Mithen 1990). Assuming they were, they also were likely to have shared their large-parcel meat at the band level (Erdal and Whiten 1996), whether scavenged or hunted: this means of variance reduction seems to be universal among extant foragers who remain nomadic (Kelly 1995; Wiessner 1996).

What about Paleolithic environmental differences? For one thing, the planet's richest resources were available to foragers, and for another their political environment did not include warlike tribal people who harvested domesticated food and lived in much larger, segmentary groups. In addition, periodically there were radical fluctuations of climate, stemming from cyclical temperature changes that affected climates profoundly and as often as every few thousand years (Potts 1996). These perturbations presented Late Pleistocene foragers with a wide variety of environmental conditions: a dynamic dimension, not observed today, included cycles of increasing scarcity but also ones of increasing opportunity to colonize newly warming areas. These changing biomes surely dislocated populations locally or required the invention of new subsistence strategies, and they also favored selection of a "generalist" brain (see Potts 1996).

Could such conditions have stimulated serious political tensions between bands? In discussing the possibilities, E. O. Wilson (1975) broadened the ethological notion of territoriality to include behaviors other than strict marking, patrolling, and defense of territory, and among many extant foragers there are clear signs of lesser degrees of resource defense (see Wilmsen 1973). In this context Kelly (1995) discusses general considerations of economic defensibility (Dyson-Hudson and Smith 1978) and specific defense strategies that employ either restrictive social boundaries or active perimeter defense (Cashdan 1983). It is clear that in spite of their rather unstable structure (see Palmer et al. 1998), extant bands can become highly xenophobic (LeVine and Campbell 1971). Where environmental factors favor this outcome they may compete directly at levels that are homicidal, and there is a strong individual tendency to exact vengeance for a kinsman. If a homicide takes place within the group, vengeance usually is avoided by the murderer's moving away (Knauft 1991; see also von Fürer-Haimendorf 1967). However, when an individual of one group kills a member of another group the tendency is to take vengeance collectively (e.g., Balikci 1970; Lee 1979), and avoidance is difficult. This means that *inter*-group homicide tends to breed further homicide. Many of the original killings involve a man competing with another man for a female partner (see Kelly 1995; Knauft 1991), so we must also consider the possibility that some kind of group raiding for women took place prehistorically, either because women were scarce as marriage partners or as a side-effect of other types of conflict.[4]

Let us project these overall tendencies back into the Upper Paleolithic and consider the fact that hunter-gatherers then had the choice of the world's best environmental resources, that they were able to utilize such environments in a stable manner during "benign" epochs lasting sometimes for several thousand years, but also that every so often many of them were obliged to adjust to radically new conditions, and sometimes to move or perish, as glacial episodes came into play. In this connection, aside from a constant equatorial tropical zone that was periodically compressed quite radically as glaciers advanced, there were prolonged cooling periods when woodlands, savannas, or tundras replaced forests and certain areas became "arctic" (see Potts 1996). This increased the dependency on meat and stimulated a need for bands to be large enough to engage in efficient variance reduction.

If Upper Paleolithic humans had the same propensities to defend needed resources as modern foragers do, and this seems very likely, it is possible to make some educated guesses about what happened as biomes were radically transformed at different phases of climatic cycles. In adjusting to cooling climates, people might have stayed in place and changed their subsistence and political strategies in the face of growing scarcity, or possibly they could have engaged in long-range migrations, perhaps by following the migratory animals they hunted or scavenged. If they stayed in place, one strategy would have been to increase their home range at another band's expense. If they moved, they might have invaded the territories of other hungry bands as they migrated. In either case, direct conflict between bands was likely to escalate because established patterns of resource defense were being disrupted just at a time when carrying capacity was changing for the worse. In adjusting to warming climates, it seems likely that during the earlier part of the cycle the colonization of new lands might have been relatively noncompetitive as bands spaced themselves widely. However, after several thousand years of population growth, bands in such rich environments would have become subject to serious crowding. This, too, could have raised the degree of interband competition—on a periodic basis.

Given these possibilities, is there any direct evidence of Paleolithic bands wiping out—or at least decimating—other bands? Keeley (1996) has documented archaeologically the rise of warfare in the Neolithic, but we must define "warfare" rather carefully. With extant nonliterate societies, there seems to be an empirical continuum (see Boehm 1986) that runs between feuding and raiding, and also between each of these and warfare involving intensive battles between groups, or massive genocidal surprise attacks. Keeley seems to be most interested in *intensive* warfare of the genocidal type, and convincing evidence of defensive ramparts and large massacres is found in the Neolithic. In the Mesolithic, in well-researched areas where humans buried their dead there also is evidence of armed combat, and of possible massacres in which children and women were dispatched. Between 36,000 years ago and the beginning of the Mesolithic, there is ample evidence of sporadic casualties associated with weapons (see Keeley 1996). But such single homicides can be accounted for by within-group execution of deviants or interpersonal quarrels at close quarters, so the findings tend to be ambiguous even though one casualty (Aurignacian) was a child, clearly killed by a weapon. In the earlier Upper Paleolithic, albeit with far fewer skeletal remains, evidence suggestive of outright massacres simply is absent. But available facts fail to rule out lesser intergroup hostilities—attacks sufficient to influence the relative sizes of nearby bands significantly over periods of mere decades. For example, killing of single intruders because of perimeter defense or cautious raiding by small parties for vengeance would leave no evidence that could be differentiated from that left by killings within the group. In extant bands the latter do occur at high rates (see Knauft 1991), so the scant pre-Mesolithic data remain quite ambiguous.

If we turn to ancestral-ape possibilities for "warfare," it is well documented that the perimeter defense activities of chimpanzee communities at Gombe (Goodall 1986), Mahale (Nishida 1979), and surely elsewhere, can result in successive decimations of territorial communities that rather quickly eliminate the males of one group, along with some of its females. These male patrolling activities have been likened to human "raiding"

(Boehm 1992; Manson and Wrangham 1991), in the sense that a large group tries to sneak up on an enemy and kill one or two of them without any loss to the raiders, or seeks to acquire stranger females. Chimpanzees also may move into enemy territory in larger, mixed groups ("excursions") to exploit the natural resources of strangers (Goodall 1986). So far, bonobo research shows xenophobic tendencies that seem similar but substantially less developed, with no direct evidence of killing between groups (Kano 1992; see also Stanford 1998).[5]

Classical modern warfare between nations is based largely on massed battles (e.g., Wrangham 1999), but with extant tribal groups I have suggested that raiding and feuding are not readily separated from each other in practice, nor from warfare. Turton's (1977) rich description of Mursi pastoralist-nomad "warfare" demonstrates this nicely, and there are many similar tribal examples (e.g., Boehm 1983; Chagnon 1983). I emphasize that even nonintensive, hit-and-run tribal raids can have long-term territorial and demographic consequences (e.g., Turton 1977; Meggitt 1977; Chagnon 1983, 1988b; see also Sahlins 1961; Soltis et al. 1995). Indeed, the cumulative consequences can be similar to those resulting from larger-scale, more *intensive* tribal warfare (e.g., Bohannan 1954; Kelly 1985; Soltis et al. 1995).

If we turn from tribesmen to extant hunter-gatherers, many engage in some type of lower-level conflict between groups (see Ember 1978; Kelly 1995). Lee's (1979) Kalahari descriptions demonstrate that prolonged exchanges of revenge killings can have significant demographic consequences within a decade, even though basically this affects males. With Kalahari foragers there is the possibility of recent cultural influences from nearby tribesmen, but similar patterns prevail with other foragers, such as many of the Inuit speakers of the Arctic (e.g., Balikci 1970) and many Australian Aborigines (see Berndt and Berndt 1964). This type of sporadic but fairly frequent intergroup homicide affects relative group size directly, and it also affects the long-term control of resources by bands, and therefore the reproductive fates of both females and males.

It is logical that early Anatomically Modern Humans might have developed similar interband tensions with respect to scarce resources, critical water supplies, and possibly females, and that such tensions would have been expressed through social boundary defense, perimeter defense, or small-scale lethal raiding. Pressure on carrying capacity, proximity of bands, and patterns of male competition for women would have determined whether homicidal exchanges rose to the level of raiding in small parties, but it is far from unlikely that sometimes raids were exchanged over periods of years. I emphasize that human tendencies to retaliate (Daly and Wilson 1988; see also Boehm 1989; Knauft 1991) are expressed prominently by extant foragers, both within and between bands (e.g., Balikci 1970; Lee 1979; see also Kelly 1995); thus, a conflict that begins over resources can be prolonged, or escalated, on the basis of vengeance.

This political scenario applies not only to cooling cycles but to later phases of the warming cycles as well. I emphasize that hunter-gatherer populations are capable of growth (Hayden 1986), even though marginalized bands under extant conditions seem to stay below carrying capacity (Kelly 1995). 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. I emphasize that at very close quarters band-level avoidance would have been difficult.

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.[6] Potts (1996:157–158) singles out the last completed Pleistocene "interglacial" period, which lasted for 56,000 years, ending at 72,000 years B.P., and shows that, as measured by oxygen isotopes, there were ten unusually sharp climatic oscillations within that period. These oscillations would have changed biomes radically, at intervals ranging from a few thousand to nearly ten thousand years. On an evolutionary time scale, 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.

One ultimate effect of all this environmental change was the substantial and recurrent long-distance displacements of *Homo erectus* and *Homo sapiens* populations which are firmly supported by the archaeological record (see Tattersall 1999). Unfortunately, we cannot examine extant foragers to see how drastic climatic changes might affect their carrying capacity, level of political conflict, and annual migration patterns, for recent climatic stability—and often circumscription by other cultures—rule this out. Indeed, we have seldom been privileged to report on extant mobile hunter-gatherers when they are coping with severe eco-stress or crowding, and we have not seen them engaging in long-range migrations in search of better opportunities or encountering bands of complete strangers. But toward 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.

Was elevated group selection likely? A plausible case can be made for significant conflict levels that were closely coordinated with certain phases of climatic fluctuation. However, we have seen that group selection arguments require not only decimation or near extinction of groups but patterns of migration and propagation that lead to the formation of new groups which vary genetically. Such details are difficult to guess about prehistorically, but by Wilson and Sober's (1994) criteria, demographically unstable Upper Paleolithic bands would seem to have been reasonably adequate as multifamily units of between-group selection. Thus, it seems very likely that a population sharing the same gene pool would have been structured into groups whose members tended to share the same fate, that the groups were in a position to replace one another, that the groups had some degree of long-term membership stability, and that the groups were not very large.[7] Presumably, these groups were subject to growth and fissioning, but also to decimation and recombination, with ample opportunities for dispersal.

Unlike the "pleiotropic subsidy" hypothesis, by which generous behavior is merely a phenotypic side-effect of genetically based nepotism, this "warfare" hypothesis provides for selection forces that might have directly supported altruistic traits. However, even if between-group selection was significantly amplified by intergroup conflict, selection at this level was not likely to have been *sufficiently* competitive with within-group selection for altruistic traits to be robustly supported. I say this because it seems very unlikely that group extinction rates came close to equaling individual extinction rates. Indeed, if free riders were at liberty to express their opportunistic genetic tendencies, altruistic traits would have needed some further (and major) source of direct support.

As will be seen in the next section, both the need for substantial empowerment of between-group selection and also the free-rider problem can be resolved by postulating an egalitarian syndrome that was shared by all Anatomically Modern Humans until well into the Neolithic.

HYPOTHESIS III: THE EGALITARIAN SYNDROME AND ITS EFFECTS

I now turn to an evolutionary hypothesis that admits of higher plausibility than the two treated so far. Mobile hunter-gatherers are remarkably uniform in their social and political life, and I shall dissect the egalitarian syndrome that dominates their social, political, and economic affairs to show that morally based egalitarianism could have been a major influence on natural selection process in the Upper Paleolithic. First, however, we must explore the cognitive and cultural capacities that were necessary to such a pattern, notably, two closely related types of human "intelligence."

Political Intelligence

Over the past decade there have proliferated a number of very specific, "modular" approaches to understanding human psychology as an interface between natural selection and behavior (e.g., Barkow et al. 1992). Here, a more rough and ready definition of intelligence will suffice: this refers to the human capacity to pool intellectual resources and solve practical problems (see Boehm 1978), be they ecological, social, or political. As I focus on some of the more general aspects of this problem-solving ability, the rubrics "political intelligence" and "actuarial intelligence" will apply to behavioral function, not to brain physiology as we know it today.

First, let us consider what I have called "political intelligence" (Boehm 1997a)—the ability to understand complicated political systems and manipulate political situations by acting individually or in coalitions. Hunter-gatherer coalitions can be quite large, for as moral communities nomadic bands often act all but unanimously when they coalesce aggressively to deal with deviants. Labeling the alpha role as deviant, these egalitarians regularly reverse the flow of power in their groups by ganging up on individuals who seem too interested in, or bent upon, self-aggrandizement. Small societies that behave in this way are clearly "intentional" (Boehm 1993), in that an indigenous cognitive "blueprint" is guiding behavior. To regularly suppress hierarchical tendencies, and do so systematically in a wide variety of environments, requires a formidable political intelligence and a well-focused sense of political purpose (Boehm 1997b).

I emphasize that egalitarian society did not stay in place just through blind continuance of some new political invention (e.g., Boyd and Richerson 1985; Campbell 1965b). Rather, it arose as prehistoric hunter-gatherers came to understand their own political dynamics and opted for individual autonomy of the type described by Cashdan (1980) and Gardner (1991). As moralistic groups, they decided (in effect) to set aside the opportunity for individual domination, so that all the main political actors in a band could remain at parity. This unorthodox political approach could have been invented in the Middle Paleolithic or earlier (Knauft 1991; see also Boehm 1982), but the necessary political intelligence surely was in place by the Upper Paleolithic (Boehm 1997b, 1999a).

Today, this hunter-gatherer commitment to political parity (see Fried 1967) expresses itself similarly on different continents, wherever foragers are nonsedentary, and it continues with the numerous tribesmen who succeeded foragers in the Neolithic (see Boehm 1993). In fact, there is a direct line of historical transmission, through the League of the (tribal) Iroquois (see Weatherford 1988), that culturally links modern democratic politics with Paleolithic political patterns (see Boehm 1999b). This antihierarchical bent of Paleolithic humans, expressed in the form of political egalitarianism, had profound effects on natural selection process.

Actuarial Intelligence

There is a second, highly "stochastic" type of intelligence that figures not only in the egalitarian syndrome we are about to examine, but in the ways that free riders are coped with in hunter-gatherer bands that cooperate extensively. In calling this "actuarial intelligence," I refer to the wider capacity of nonliterate people to intuitively understand—and manipulate—various types of "systems" they are engaged with (see Boehm 1978, 1991, 1996; Mithen 1989, 1990). With respect to the natural environment, foragers understand the quantitative relationship between rainfall and plant growth or faunal abundance, and they understand annual seasons. They actively exchange microenvironmental information, and they fine-tune decisions that help their well-cognized foraging strategies to become substantially congruent with optimal patterns that behavioral ecologists adduce from the behaviors of other animals (e.g., Smith 1987, 1991; see also Mithen 1989, 1990). In this important sense, they are intuitive "systems theorists."

With respect to the immediate political environment, they not only understand the workings of their own political system well enough to keep it egalitarian, succeeding in spite of strong forces that make for hierarchy (Boehm 1993, 1999b), but they also create strategies of social boundary defense or perimeter defense, and may retaliate politically against other groups in order to be able to travel abroad safely (e.g., Balikci 1970). Political intelligence and actuarial intelligence are closely related, and both involve complex insights and calculations.

Actuarial intelligence also operates importantly in social cooperation: mobile hunter-gatherers universally share their larger game, even if the available animals are relatively small (see Kelly 1995). Scholars who study hunters think in terms of "variance reduction" (e.g., Smith 1988; Smith and Boyd 1990; Winterhalder 1986), and foragers themselves appear to be thinking similarly (see Mithen 1989). It would appear that even the best hunters realize their major kills will often be sporadic, while lesser hunters have still more to gain by pooling their products at the band level. It could be argued that foragers are just sharing their meat blindly, as a matter of cultural habit, but when game becomes extremely abundant the sharing tends to stop (e.g., Binford 1978)—to be taken up again when variance reduction makes sense actuarially.

This well-routinized, cognized approach to variance reduction is widespread. For example, Kelly (1995) has discussed how on various continents customs are kept in place that diffuse ownership of meat, or place its distribution in charge of individuals who did not acquire the prey. While it is likely that philosophically gifted informants might spell out something like "variance reduction" as the criterion, such goals often remain "intuitive"—and ethnographically difficult to elicit. However, the Netsilik Eskimo system of sharing seal kills exemplifies nicely how actuarial principles come into play (see also Boehm 1999b). During the winter sealing season, the Netsilik are dependent on large game and they readily share meat within families or extended families. However, among unrelated families they have created a far from spontaneous system of sharing, one that shows great sophistication of design (see Balikci 1970; Van de Velde 1956). Each hunter has a specified partnership with every other unrelated hunter, by which he shares reciprocally just one seal body part, such as the flipper, belly, or head. The overall effect is that every seal is distributed on a highly regulated basis to every family in the camp. The system essentially ignores the major differences of hunting prowess and luck that prevail; rather, the sharing is "equalized" so that the reduction of family variance in meat intake is maximized.

The fact that band members sometimes assist unrelated people in the band who are incapacitated (see Kelly 1995), and hope to be similarly assisted if their own numbers come up because of being wounded, maimed, or ill, or because of aging, is another expression of actuarial calculations that surely underlie rules developed by groups. The parallel thinking behind these informal "safety nets" and modern institutionalized ones is worth noting. Hunter-gatherers would appear to believe in insurance as a form of risk reduction (e.g., Cashdan 1990): you pay your contributions and are later taken care of even if you have exceptionally bad luck. However, in both systems there are coverage limits.

Hunter-gatherers cut off individual benefits precisely when payouts threaten the overall welfare of the system's members. Individuals who cannot walk are often left behind by their families or bands at migration time, and in the Netsilik case the reasoning is quite clear: in winter migrations their sleds carry equipment necessary for survival, and the number of dogs is limited in terms of food supply (see Balikci 1970). Their death, by freezing, is quick and relatively painless. For many nomads, individuals incapable of locomotion create a serious burden (sometimes a dangerous one), and if their condition is chronic there is no point in further investment. In benign climates, often those who cannot walk are killed to spare them from lengthy periods of suffering after they are abandoned.

Kelly (1995:202) tentatively seems to agree that conscious actuarial calculations are taking place:

> It is . . . clear that the costs and benefits of sharing are analyzed over some period of time, taking into account past experiences and future expectations. These costs and benefits are probably analyzed in terms of the degree of correlation between foragers' efforts and the amount of day-to-day variance in those efforts. Individual foragers may share resources to reduce the risk of going without any food in the future, or as an exchange for complementary resources, sexual favors, or support in old age.

In discussing Winterhalder's (1986) model, Kelly (1995:179) refers to "hunter-gatherer social security networks," and he suggests that these people may be planning for their retirement as they invest in sharing networks at earlier stages of their life cycle. He mentions Biesele and Howell's (1981) point that favors and gifts given in youth and middle age ensure a return in old age, and he ends with a call for further research.

Kelly (1995) shows that cooperation extends beyond sharing within the band. When microenvironmental variation exists, such that one band is hungry while its neighbor is well fed, foragers create systems that favor affiliation between friendly bands; people can move to where resources are less scarce even if this means asking to use resources normally exploited by neighbors. Wiessner's (1982) study of Kalahari forager *hxaro* exchange systems describes a mechanism by which people have "excuses" to make such demands on (temporarily) better-off neighbors who are trading partners. However, where microenvironmental variation is low people in large areas fall on hard times together, and as a result Kelly (1995) believes they develop a "territorial" approach to guarding the resource areas they normally use—one that works against intergroup assistance in hard times. Ultimately, both patterns can be attributed to sound actuarial insights of hunter-gatherers.

There would appear to be three types of safety nets. Prominent, and most reliable, is the family. If you are statistically fortunate, you will have coresident adult children to support you in case of mishap. This type of support is explained by kin selection, and predictably other relatives will tend to avoid giving help if immediate family can handle the burden (e.g., Thomas 1958). Next we have a network of specific "investments" made in a context of rather imprecise but well-remembered reciprocal exchanges between nonrelatives during a lifetime of sharing (e.g., Wiessner 1982). This approach is far from universal, and being imprecise it is only partly explained by theories involving exact reciprocity. The third safety net derives from the generalized ethic that no band member should be neglected in a time of difficulty—unless the costs of helping are prohibitive. Kelly has pointed to the paucity of data in this last case, but I can supply an unpublished anecdote from my 1960s fieldwork with pastoralist Serbs in southern Hercegovina. In the isolated Christian *pleme* (tribe) with whom I lived, the almost 1,800 people basically were self-sufficient economically. There was a relatively vigorous old woman in her eighties, who was the victim of statistical sport: she "had no family left, whatsoever." On a daily basis, she moved from one house to another, walking with two canes, to be a guest for the night. It was understood that she would not stay for more than a night, for people did not want to become exclusively responsible for her in the normal family sense, but no one ever refused her a night's haven. This "rotation" arrangement, far less satisfactory than being cared for by relatives, enabled her to survive for years.

These band-level safety nets are difficult to explain genetically. Ideologically, they bear a noteworthy resemblance to the family and kin-based systems, but in terms of genetic cost-benefit analysis they involve unreciprocated assistance to non-kin. Not only do these nonrelatives exchange goods and services unpredictably and unevenly on a lifetime basis (e.g., Alexander 1987), but with a constantly changing band composition people can live the productive portion of their life in one or more bands and then "retire" in still another. Palmer and colleagues (1998) have pointed out that foragers over-perceive the unity and permanence of their bands. One reason for this may be that they are conceptualizing the band as a unit of social security—and as a fallback unit of moral obligation.

To summarize, these political and social applications of a rather *generalized* human intelligence involve thinking inventively, and flexibly, in terms of "systems." There is no reason to believe that early Anatomically Modern Humans were very different from ourselves in this potential, and this capacity helped them to redesign their political society. It also enabled them to set up effective security nets, particularly (and universally) with respect to the sharing of large game kills. In understanding these ongoing systems that they created and maintained, they were in a position to readily identify, and try to control, the severe damage that bullies or cheaters can do to such enterprises. The well-strategized suppression of more serious types of free-riding behavior will play an absolutely critical role in the arguments to come, but first let us consider the impact of egalitarianism, on natural selection processes.

Political Suppression of Phenotypic Variation

The "egalitarian syndrome" (Boehm 1997b) is characteristic of all extant foragers who remain nomadic. Aspects of this syndrome have been similarly described by a number of ethnologists (Boehm 1982, 1993; Cashdan 1980; Fried 1967, 1975; Gardner 1991; Knauft 1991; Lee 1979; Service 1962, 1971, 1975; Woodburn 1982; see also Middleton and Tait 1958), who agree that mobile hunter-gatherers exhibit the following: a relatively low level of male competition and hierarchy with low-key leadership; a consensual mode of making cooperative decisions, and a strongly egalitarian ethos.

Recently, in a variety of contexts I have suggested that Upper Paleolithic hunter-gatherer moral communities had profound effects on natural selection process because they were politically egalitarian (Boehm 1997a, 1997b, 1999a, 1999b). In effect, egalitarianism involves political hierarchies becoming "reversed" as the subordinates manage to keep the group's alpha types under their thumbs (Boehm 1993, 1994b; Knauft 1994; see also Erdal and Whiten 1994, 1996), and as a result the reproductive advantages of stronger or more assertive males are drastically curtailed. This could have affected phenotypic variation at the within-group level quite profoundly (Boehm 1997b).

It is phenotypic variation that, with extinction rates, drives natural selection (E. O. Wilson 1975). In building mathematical models, sociobiologists, behavioral ecologists, and many ethologists tend to assume that phenotypic variation and genotypic variation are isomorphic, and therefore they do their modeling solely on the basis of genes (see Wilson and Kniffen, this issue). This simplifying assumption may work with species that lack morality, but human moral communities regularly interfere with individual behaviors, ones based on lust, greed, or dominance, that bring reproductive success to the perpetrators unless they are "policed." Such policing can be very effective (see Boyd and Richerson 1992), and if it suppresses competition and domination it is sure to reduce phenotypic variation among individuals (Boehm 1997b).

In the Upper Paleolithic the effect was that direct competition among individuals was seriously diminished, and phenotypic variation at the within-group level therefore plummeted. How far did it fall? Let us compare a typical egalitarian group with one that is not. The modal nomadic band contains perhaps six to twelve families, some of which are related and some are not (see Kelly 1995). However, a band also may be part of a cluster of bands within which social visiting and sharing of resources are frequent while relations between adjacent clusters are distant or unfriendly (e.g., Heintz 1972). Within a band or band cluster, heads of households are considered to be politically equal even though individual differences of ability and productivity are freely acknowledged (see Fried 1967). Polygyny is often found to a moderate degree (see Kelly 1995), and in a few cases it can become extreme (e.g., Hart and Pilling 1960), but basically the adult males have just one wife. The entire group is prone to cooperate, and in sharing out meat (see Erdal and Whiten 1996) a decentralized system is used: there is no well-developed political authority except, often, within the family. In comparison with other animals, this suggests an "egalitarian" political order as ethologically defined by Vehrencamp (1983), rather than a "despotic" one like that of chimpanzees—or humans living in chiefdoms.

In Vehrencamp's sense, the common ancestor of humans and the three African great apes was innately "despotic" (Tiger 1969; Tiger and Fox 1971; Boehm 1982, 1999b; Knauft 1991; see also Wrangham and Peterson 1996). Significant reproductive advantages went to those of high rank—as usually takes place with other despotic primates (see Ellis 1995) whose natural propensities to domination are not being suppressed in a morally focused way. The result was a high level of within-group variation, determined by rank. The intentional egalitarianism of humans changed this radically because people who otherwise would have been subordinates banded together to suppress power roles within the band. However, the change took place basically at the level of phenotype (Boehm 1996), for humans remained a species that readily learned dominance and submission behaviors. It was just that the locus of manipulative power shifted from alpha types to a rank and file who successfully used collective domination to resist being dominated individually. In effect, an innately despotic species, one likely to form strongly led social dominance hierarchies, used its political intelligence to forcefully eliminate bullying behavior—and thereby drastically reduced phenotypic variation within its groups.

The hominid precursors of prehistoric egalitarians surely were despotic (see Knauft 1991; Boehm 1999b) and therefore exhibited high variation within groups. When humans recently lost the egalitarian resolve to curtail competition and domination, or decided that they actually liked being "bossed" by generous or charismatic patrons, phenotypic variation within groups shot up again. One has only to compare mobile, egalitarian hunter-gatherers with modern people who have become extremely hierarchical (e.g., Betzig 1982) to see that the differences can be extreme, while even certain sedentary hunter-gatherers, such as the Kwakiutl, developed chiefs whose lineages were considered to be noble, held slaves, tolerated substantial polygamy, and favored economic competition instead of largely suppressing it (see Rosman and Rubel 1986).

With such comparisons in mind, I conclude that a protracted egalitarian phase of human evolution involved a really marked flattening of phenotypic differences, particularly among male household heads. This reduction of within-group variation was substantial, but far from total. Superior hunters might still gain special advantages in mating (e.g., Hill and Kaplan 1988; see also Chagnon 1988a; Hawkes 1991), sporadic polygamy was present, and certain other kinds of social competition continued (see Fried 1967; Flanagan 1989). But the protracted, consistent, and substantial political leveling under egalitarianism was significant with respect to the potential selection of altruistic genes, for if you drastically reduce variation *within* the group, you make it easier for selection at the between-group level to support traits that are altruistic (see E. O. Wilson 1975; Wilson and Sober 1994).

Consensus Seeking Further Suppresses *Within-Group* Variation

Every year, typical nomadic foragers make multiple migration decisions as bands. These decisions are consensual because the constituent families understand, actuarially, the benefits of staying together: protection from animal or human predators; cooperative hunting possibilities; the sharing of large game; and (always pleasurable) sociality. Selecting basic subsistence strategies as bands further weakens the force of gene selection within these groups: instead of one family trying its luck in (arbitrarily) "kudu country" and another in "antelope country," an entire band normally migrates to the same locale, and then typically all the families operate within that parameter. In this context, egalitarian groups tend to place pressure on minorities to follow the majority decisions (Boehm 1996)—even though basically every family is politically autonomous. Prehistorically, it would appear that bands operated similarly (Mithen 1990). The effect was that within bands behavior differences among individuals (see Mithen 1989) could be very useful to the band, in terms of providing a variety of decision alternatives, yet because of consensus seeking the band's *basic* subsistence strategy usually was standardized.

I do not wish to draw a caricature. At certain seasons some bands atomize temporarily into family units, and when bands migrate it may be feasible for a dissenting family simply to change bands before (or after) migrating. There are even a few Australian desert bands that face such sparse resources and great environmental unpredictability that most of the time they operate basically as families (Gould 1982), while a few sedentary (but politically egalitarian) foragers in northern California live together in settlements yet function economically merely as families because they store food (Gould 1982). But the great central tendency is for the entire band to migrate as a unit, and to share its large game kills. It is true that once a group migration is completed, individuals and families can vary their hunting and gathering microstrategies locally, but with basic strategic decisions being made by entire bands, the potential phenotypic variation in subsistence pattern is significantly curtailed if one compares bands with unorganized clusters of families foraging on their own.

Effect of Consensus Seeking on *Between-Group* Variation

The widespread tendency of band members to pursue basic subsistence strategies on a unanimous basis also affects the force of selection at the between-group level (see Boehm 1997b). As consensual decision units, nearby bands usually are in a position to vary significantly with respect to how they exploit their environments. In more favorable Paleolithic environments there was likely to have been a considerable range of potential strategies that foragers could pursue successfully in a given locale, and their choices would have varied according to the subsistence dilemmas they perceived, and how they resolved them. Predictions about game availability, rainfall, physical comfort or discomfort, and perceived health risks are likely to have figured in such cognitively constructed dilemmas.

Potts (1998) has proposed the term "variability selection" to cover the evolution of our human degrees of behavioral flexibility, which came as a response to highly changeable Paleolithic environments. The evolved human defense against extreme and repeated climate changes was an unusual capacity to cognize natural environments and to modify or substitute subsistence strategies successfully. Because this flexible capacity was so heavily cognitive, and because it promoted trial-and-error innovation, similar groups facing similar exigencies were likely to differ sometimes in the local subsistence strategies they chose. When nearby bands are setting up their choice dilemmas differently, or set up their dilemmas similarly but then make varying choices, group differences in reproductive success are likely.[8]

Even in present environments that are relatively stable, a band that guesses wrong in going after giraffe as opposed to kudu, or guesses wrong about where scarcity of rainfall is likely, could end up losing some ground demographically and, once in a while, experiencing famine. In less favorable environments, or during severe droughts or other perturbations, such decisions could become immediately crucial to reproductive success for entire groups, as varying emergency decisions could subject one band to serious decimation or even outright or near extinction while another survived far better (see Boehm 1996, 1997a, 1997b). Because total extinction of bands is not necessary for the robust operation of natural selection at the between-group level (Wilson and Sober 1994), variance in population growth (or decline) could suffice to generate significant forces in this direction.

To explore prehistoric specifics with respect to migration, dispersal, and formation of genetically varying propagules (see Wade 1978) is beyond the scope of this paper, but the possibilities are obvious. Growing bands are obliged to fission when they outrun resource availability—or if they become dangerously factionalized (see Boehm 1993). It is quite conceivable that altruists or free riders tend to stick together at such points, and that subsequent rates of natural increase could vary along this dimension. Likewise, when bands are decimated by environmental misfortune there may be a differential culling of altruists and free riders. Furthermore, Bowles and Gintis (1998) have suggested that ostracism of flagrant shirkers could have affected band composition in ways that were relevant to the operation of between-group selection.

During climatically stable periods, elevated group selection would seem to have been possible, prehistorically, whenever routine decision making varied among adjacent bands in ways that were reproductively consequential. In estimating such variation, one must keep in mind that during warming cycles many bands were exploiting environments so rich that a diverse array of adaptive strategies could succeed. This means that in spite of tendencies to borrow culturally, different bands residing in the same area could have followed subsistence strategies that varied substantially. During cooling cycles, the range of potential adaptive strategies was likely to have narrowed, but emergency decision making was likely to have been frequent, or chronic, as people were obliged to improvise radically or seek new home ranges, and followed differing strategies in doing so. It seems likely that large numbers of foragers perished at such junctures, and that bands with differing strategies would have been affected differentially.

Even in our present environmental context, which is relatively stable, many extant foragers would appear to be facing recurrent and serious problems with respect to subsistence (see Ember 1978). Unfortunately, few have been studied at such times. If we return to Potts's (1996) analysis of the highly unstable 56,000-year "interglacial" period during which Anatomically Modern Humans were diffusing worldwide, within each of the ten pronounced subcycles people were faced with stages that would have powerfully stimulated their capacity to innovate strategically as groups—whether the context was ecological or political. Because their strategic experiments would have varied, the degree of success or failure also would have varied—at the band level. This substantial variation can be laid at the doorstep of the large brains humans had developed at that juncture. Differences of intelligence, experience, information sharing, collective decision-making acumen, and capacity to enact complex decisions all helped to make Paleolithic bands into effective group vehicles of selection (see Boehm 1978) as they coped with a changeable variety of environmental constraints and possibilities.

This is not to say that every ecological emergency will result in a collective (i.e., multifamily) attempt to cope. Sorokin (1942), Laughlin and Brady (1978), and Dirks (1980) agree that for humans, famine has variable effects that can amplify either cooperation among families or familistic selfishness. This depends not only on the culture, but on the stage of response to scarcity (Dirks 1980). The total literature on human disaster coping is small, and for hunter-gatherers only a few reliable ethnographic accounts exist (see Laughlin and Brady 1978).[9] However, when neighboring groups do cope with unusual scarcity, and do so by acting as entire bands that choose different strategies, this should substantially raise phenotypic variation at the between-group level of selection—and do so just at a time when differential decimation is likely. Of course, when bands "atomize" socially under stress, such variation is drastically reduced.

I have assumed that foragers' decisions tend to be reasonably "rational" from a strictly ecological standpoint (see Mithen 1989). However, the more "rational" decision makers don't always win such "races." Decisions have unanticipated and far from optimal consequences (Boehm 1978)—partly because human rationality is bounded (Simon 1983), partly because blind luck can enter the equation to defeat highly logical decisions or enhance less logical ones, and partly because nonoptimizing folk beliefs (e.g., zebra meat is unwholesome) may hold sway in certain contexts (e.g., Mithen 1989). But so long as intentionally guided group strategies vary, and such variation leads to differing demographic consequences, this will boost variation at the between-group level and assist the selection of altruistic traits. In this connection, both routine and emergency decisions can elevate variation available to between-group selection.

Problems with the "Band"

We must return, now, to the question of bands as apparently "flawed" yet mechanically effective group vehicles of selection. Palmer and colleagues (1998) have raised an important definitional question, insofar as "bands" surely exist more in the eye of beholders—be they ethnographers or hunter-gatherers—than in fact. Both use static typologies to describe less than stable groups as though they were enduring. Demographically, husbands and wives with their dependents form far more permanent social units, while band compositions tend to change considerably over time. Depending on the distribution and quantity of resources (see Gould 1982; Kelly 1995), families generally can join the bands of either set of in-laws or of any close kinsmen, and it would appear that rather frequently exogamy prevails (see Kelly 1995), partly as a way of creating ties that may be useful in hard times. The back and forth nature of this visiting must be factored into any mathematical modeling that uses bands as units of selection, as must general patterns of endogamy versus exogamy, and any cooperative networks that follow kin ties rather than band boundaries.

Do such "instabilities" preclude selection taking place between groups? Lee (1979) has shown among the !Kung that a multifamily core of people retains a long-term proprietary relationship with respect to important local resources, and this is likely elsewhere. Furthermore, the small clusters of bands identified by Heintz (1972) rigidly exclude strangers. Where this nexus-type organization prevails, between-group selection could be operating at both the band and band-cluster level, with the cluster being a more stable and well-bounded social unit and one far less subject to gene transfer between groups. Where perimeter defense prevails, this too will tend to firm up boundaries between bands. The conclusion is that in their *routinized* activities, bands or band clusters exhibit enough long-term continuity so that between-group selection can operate much more strongly than is assumed by the many scholars who simply dismiss selection at this level (see Wilson and Sober 1994). In emergencies—at least during the cooperative phases—bands may serve as effective vehicles for rapid and radical between-group selection, precisely because desperate people may be driven to experiment (Boehm 1996, 1999b) and they have the habit of sticking together in order to cooperate.

Summarizing the Effects on Variation

By definition, "altruistic genes" are undercut by within-group selection and are supported by between-group selection, so we may consider these as two separate "engines." If we compare egalitarian societies with nonegalitarian societies, among egalitarians the within-group engine has lost a great deal of power because the variation that fuels it is diminished so radically by the egalitarian syndrome. At the same time, the between-group engine becomes significantly stronger whenever nearby groups are choosing different subsistence strategies—or different political strategies.

The egalitarian syndrome drastically reduced variation within multifamily bands because male competition and despotic domination behavior were directly suppressed on an intentional basis. In addition, within-group variation was reduced by consensual decision making. At the same time, adjacent or nearby bands were free to vary their ecological and political strategies, raising variation at the between-group level. Beginning with Anatomically Modern Humans or possibly earlier, these behaviors continued for thousands of generations, and they surely had a direct and significant impact on human gene pools.

I do not wish to overextend an argument that cannot fully address important technical issues of migration, dispersal, and propagation of new groups that vary genetically. But I do believe it to be highly unlikely that within-group selection was being debilitated, or between-group selection amplified, to a degree that the two levels of selection were operating with anything like equal force.[10] If we leave out the warfare hypothesis, what we are talking about, here, is some significant amplification of between-group variation and a very substantial debilitation of within-group variation. This selection scenario provides altruistic traits with much better support than they receive in nonegalitarian human groups, where subsistence decisions are made by families but free riders remain an absolutely critical problem.

COPING WITH OPPORTUNISTIC FREE RIDERS

With respect to natural selection, group-beneficial behaviors can be logically divided into three types (see Sober and Wilson 1998): (1) those that are useful to both group and individual reproductive success; (2) those that are selectively neutral for individuals but useful to groups; and (3) the much-discussed *altruistic* behaviors that combine individual sacrifice with group benefit. I employ the term "altruistic" here as it was defined at the outset. The same goes for "free riders" as individuals who by genetic definition are prepared to aggrandize their own relative fitness by taking advantage of born altruists in the group. I emphasize that as modeled by Hamilton (1964), free riders become an all but fatal problem for the selection of altruistic genes because they so strongly outclass the altruists reproductively.

Hamilton assumed uniformity between genotype and phenotype when he did his modeling, and for humans his conclusions have been widely accepted for three decades (e.g., Alexander 1974, 1987; Ridley 1996; Trivers 1971; Williams 1966; E. O. Wilson 1975, 1978; Wright 1994). However, if one ignores phenotype to build mathematical models based on "free-rider genes" that (in theory) make for easy opportunistic exploitation of poorly defended altruists, a serious fallacy arises. As we shall see, hunter-gatherer moral communities are in a position to deny to born free riders many of the phenotypic benefits they might otherwise gain at the expense of born altruists, and sometimes actually punish them reproductively. This is the case with cheaters, but also with bullies. Both may be treated theoretically as "free riders."

Free Riding That "Doesn't Matter"

In the discussion of actuarial intelligence, it became clear that foragers are accepting significant reproductive donations from nonrelatives all the time, in the form of meat sharing when game acquisition is unpredictable, some degree of caretaking when they are incapacitated, and so on. However, not all of the people who seem to be taking free rides in band life will be *born* free riders--people who are unusually disposed to competitive opportunism.

When band members accept such donations, this might *appear* to involve the kind of free riding that drives altruistic genes to a low frequency. However, hunter-gatherers design their safety nets in a way such that the recipients of these "insurance benefits" will be sorted out by randomized life circumstances- not by the behavior genes they carry. We have seen this with sharing of meat in multifamily bands. The beneficiaries include people who were unlucky (or less proficient) at hunting that week, people unlucky enough to suffer incapacitating illnesses or accidents, people who have grown too old to forage. Such afflictions hit everyone with equal probability, so statistically the born altruists and the born free riders should be donating and taking away exactly the same benefits. We are left with an empirical question: to what extent does everyone in a band actually follow the same rules in giving and taking, and what are the reproductive consequences of trying to cheat on the system?

Curbing the Born Opportunist

By definition born free riders are innately prepared to "take advantage" of the typical hunter-gatherer "insurance systems" we have discussed—that is, to do so more than our born altruists are likely to. Before the rise of morality and egalitarianism, these hyper-opportunists were in a position to express their tendencies rather freely, in whatever context of social cooperation prevailed, for with a species that practices deception there are many ways to take advantage of one's fellows on an individual basis—even if some individual-level cheater detection is operative. In addition, a pronounced social dominance hierarchy (see Boehm 1999b) would have facilitated the ability of higher-ranking individuals to take "free rides" by relying on power rather than deceit. With this freedom of action for bullies or cheaters, significant retention of altruistic genes was highly unlikely. It would have been unlikely even if moderate levels of "warfare" prevailed and, therefore, some really significant group selection was operative.

After the moral community and egalitarianism arrived, Paleolithic bands had ways to effectively suppress free riding that was expressed phenotypically in the form of bullying or deception, and this moralistic suppression of opportunistic behavior would have placed altruistic genes in a far better position to be retained—assuming that some significant between-group selection forces were present and that within-group selection was not too strong. I emphasize that the egalitarian syndrome required the emergence of moral communities (Boehm 1982, 1997b), and that these were easily capable of identifying and sanctioning not only cheaters (Boehm 1997a; see also Tooby and Cosmides 1992) but also bullies in their role as directly competitive opportunists.

This leaves us with an empirical question. In typical bands, to what degree do people interested in taking advantage of others actually manage to get away with taking their free rides, and how does this affect their reproductive success in comparison with born altruists? While quantitative data do not exist in this area, there are both rich anecdotes and convincing ethnographic summaries that clarify how this competition between prosocially oriented cooperators and unusually selfish opportunists tends to resolve itself.

At first blush, hunter-gatherers would appear to be set up perfectly for exploitation of altruists by cheating free riders. In Kelly's (1995) discussion of the generalized sharing ethic, we have seen that this tends to be psychologically internalized in the average band member. This is the case even though some cheating occurs and competitive quarrels are likely to arise (e.g., Peterson 1993) in bands that basically cooperate over time. In this context, there are various ways that individuals prone to cheat might do so. For example, a family hides a kill instead of sharing it, or a man or woman tries to favor kin when the task is to share out meat fairly. Or a man might pretend to be lame, and thereby take a more substantial, long-term free ride on the exhausting and often risky hunting efforts of others. Or, when cooperative activities take place he can simply be slow to participate, instead of eager. If one is able to work these "scams" without detection or reaction the reproductive advantage is obvious, and over the long term this will work significantly against the retention of altruistic traits.

Because they gain so much from sharing and cooperation, the altruists will not simply disband their security net in order to protect themselves from cheaters. We have seen already that Netsilik Eskimos are seriously driven to share because of their heavy seasonal dependency on sporadically acquired large game, and other mobile foragers share their game similarly. We also have seen that Netsilik cultural rules for sharing are unusually specific, and that this discourages even small attempts to cheat at the level of meat distribution. However, even those highly elaborated Netsilik rules of exchange do not provide total protection against free-rider opportunism: a lazy man could hunt less intensively and gain much more than he put into this system, while a serious opportunist could pretend to be ill and, *in theory,* simply let others supply him and his family with seal meat. Because Netsilik men suffer very high casualties while hunting in the winter (Balikci 1970), the genes of such born free riders would proliferate decisively.

Theory does not seem to jibe with practice. The born altruists, who are more likely to cooperate according to the rules, are far from naive. They, too, harbor some tendencies to cheat, a point overlooked in most discussions of human altruism, and this makes it easier for them to identify the born opportunists in their midst. According to Balikci, self-interest, jealousy, and hostility attended routine sharing among Netsilik non-kinsmen, and if someone tried to take a substantial free ride, the tensions could result in acts of social control. Balikci (1970:176) refers to a

> general rule among the Netsilik according to which all able-bodied men should contribute to hunting, and the returns of the hunt should be shared according to established custom. Any activity in exception to this rule was bound to provoke criticism, various forms of conflict, and frequently social ostracism. Such an exception was the lazy hunter, whom the Netsilik called *nuniurut.* They were not usually less skillful than the others—on the contrary, some *nuniurut,* when necessity demanded, were very good in the chase—but they were incurably lazy. While the temporarily disabled hunter was generally helped with gifts of food, nobody liked sharing with the *nuniurut.*

Actually, Balikci identifies several types of opportunistic free rider. Condemned as deviant freeloaders are the lazy *nuniurut,* passive opportunists who fit very well with the image of selfishly opportunistic free riders modeled by geneticists. There also are *active cheaters:* able and willing hunters who take from the system of sharing but in the eyes of their disapproving partners are deviantly reluctant to give. Balikci (1970) tells of a case in which (in his absence) a man's frozen cache of food was destroyed by children of two families to whom he had previously refused food. This suggests that a perceived attempt to cheat actually could bring a net reproductive loss to the would-be free rider.

If we move to a different continent, Wiessner's description of cooperative gift exchange among the !Kung has a similar ring to it:

> Relationships that pool risk are ideally balanced over a lifetime, if constantly controlled for cheating. For example, those who have things of value but do not give are subject to social control through gossip, ridicule or ostracism. Those who feel that they are being exploited may cease to produce for a while and force others to do their share. However, it is recognized that unpredictable events will make some people unable to reciprocate adequately even in the best of times, and, accordingly, a wide range of reciprocal ties are maintained so that people will win some times, lose other times, and break even in most (Wiessner 1996:186).

While public opinion and mild censure may help to suppress opportunistic cheating, it is clear from Wiessner's and Balikci's accounts that the free-riding tendencies of some individuals become so strongly motivated that they must be ostracized, or otherwise seriously punished. Hunter-gatherers are experts at social control, and if a born free rider's opportunistic behavior is totally suppressed, he ends up having the same reproductive status as a born altruist. On a statistical basis, both are paying into the insurance system equally, and both are taking out the same benefits. If it is only fairly well suppressed, a born free rider may gain a modest advantage over his altruistic counterpart. However, if he pushes things to the point that ostracism or other severe punishment is activated, his reproductive status could actually become worse than that of the average born altruist. There are varying degrees of ostracism (e.g., Balikci 1970; Briggs 1970), but at any level the net reproductive costs are far higher for the socially victimized malefactor than for the good citizens who are in control. They invest just a little time or energy in sanctioning him (see Wilson and Kniffen, this issue), and because cheating is stimulated by zero-sum games they share the gains they have deprived him of.

The group ethic, which both promotes sharing and leads to such punitive sanctioning, has the effect of oiling the wheels of cooperation. It curbs selfish tendencies of those who are in a good position to acquire meat (e.g., Smith 1988, 1991; see also Erdal and Whiten 1996), while simultaneously encouraging them to share. However, the group's vigilance will accord with the stakes that are perceived by altruistic cooperators. In normal times, when most ethnographic observation takes place, a certain amount of "slippage" is permitted, and for that reason it appears that ultimately the "free-rider problem" might be a very serious one. However, there are several conditions under which one can predict that as insightful cost-accountants, hunter-gatherers will begin to deny meat or other benefits to deviant free riders, or actively punish them through sanctioning. One situation is when regularly shared items become scarce. Although we have few ethnographic reports, the same actuarial acumen that curbs free riders who are too consistently exploitative in normal times would be at work here. Another would be if these opportunists were starting to become too numerous in a band. Actuarial intelligence makes it easy to add up the consequences of having a band with six hunters—three of whom are *nuniuruts*. Another would be if the behavior of individual free riders was becoming both continual and flagrant. In both cases, we have negative evidence. If half the hunters in a band were trying to freeload, or if single individuals were taking blatant, long-term free rides in most bands, this would be duly noted.

Boyd and Richerson (1992) have made the argument that "punishment allows the evolution of cooperation (or anything else) in sizable groups," and with respect to cheating the name of the punitive game is "moralistic aggression" (Trivers 1971). I emphasize that there is far more to "free-rider control" than social distancing or active punishment. Foragers become identified with their own prosocial ethos, and they also desire social approval. Willing, proficient hunters universally receive respect and prestige (e.g., Hawkes 1991; Kaplan 1985; Lee 1979; see also Alexander 1987). Thus, when the ardors of hunting are at issue it is fear of sanctioning and desire for respect, working in tandem, that induce even individuals who are especially prone to take free rides to set aside their selfish tendencies. They do so most of the time, and therefore contribute like everyone else.

In short, an inborn "altruism deficiency" won't do your fitness much good in a hunter-gatherer band because free-rider suppression increases just when you have the most to gain. This includes deceptive or lazy free riding, but also, for example, trying to act as a camp bully who uses intimidation to appropriate the meat of others or deny a share to them. Among foragers, the bullying appropriation of meat is suppressed (see Erdal and Whiten 1996) precisely because bullying of any kind is sharply proscribed by the egalitarian ethos (Boehm 1993). In spite of this, suspicion, bickering, argumentation, and occasional quarreling are quite expectable in a band in which strongly nepotistic family units espouse altruistic rules of interfamilial sharing in order to reduce variance in their long-term protein supply. Blurton-Jones (1984) and Peterson (1993) have offered theories to explain the serious tensions that sometimes arise when foragers share their meat, and such tensions may be associated with attempts to take free rides. But in practice, neither lazy nor cheating nor bullying traits are likely to result in reproductive exploitation *nearly* as substantial as one would assume from abstract discussions about free riders.

The free rider's "personal problem" is that of any deviant in a small band. People watch one another's behavior closely, and they exchange information through gossiping (e.g., von Fürer-Haimendorf 1967). They add up patterns of behavior, and they pay close attention to motives. They are quick to become angry—and aggressive as a political coalition—if someone's deviance is likely to damage their collective self-interests. They have ridicule and criticism at their disposal, and they can also engage in powerful social distancing mechanisms that range from mild ostracism to ejection from the group, or even execution. Even if the deviant is dangerous they are able to handle virtually any form of deviance they are able to detect (see Boehm 1993, 1999b), and it is not difficult for them to add up the pattern if someone is regularly taking serious free rides. Obviously, opportunistic free-rider types do get away with some exploitation, but the higher the reproductive stakes, or the more persistent their pattern, or the more of them there are in the band, the more likely they are to end up with very little advantage or even a net loss. It is also worth noting that our born altruists are likely to do a certain amount of free riding themselves, which in the context of reproductive competition also helps to reduce their net losses to born free riders.

This obviously affects efforts to model the selection of "altruist" and "free-rider" genes for humans. At the level of phenotypic expression, these are far from being mutually exclusive trait categories; indeed, an artificial and extreme contrast has been created by equating genotype with phenotype and modeling just two diametrically contrastive types of gene. What we actually are likely to encounter is competition that pits selfish opportunists who are somewhat less so against selfish opportunists who are somewhat more so. The former try to police the latter by acting as a moral community that serves as a large and powerful political coalition. This means that our traditional "altruist" and "free-rider" types (as found in mathematical models) have amounted to behavioral caricatures.

Moral communities can be effective in manipulating cheaters and bullies because it takes an opportunist to spot an opportunist, and all humans are basically opportunists even though some are genetically endowed as hyper-opportunists. We are all opportunists because our species is so strongly driven by egoistic and nepotistic self-interest which stems from inclusive fitness. This same self-interest helps the vulnerable "good citizens" (the born altruists) to join together and curb the antisocial behavior of opportunistic deviants (the born free riders).

Thus, in intimate forager bands there is virtually nowhere to hide. People's dossiers are constructed and disseminated, and seriously opportunistic inclinations can be readily assessed and coped with (Boehm 1999b) because circumstantial evidence makes for a sound "criminal case." While a reasonable degree of antisocial opportunism is tolerated, serious damage is controlled quite effectively by a moral community that sorts deviants into categories such as "*nuniurut*," calculates the damage they are doing on a sound actuarial basis, and tries to manipulate their behavior accordingly.

With the "free-rider problem" largely disposed of at the level of phenotype, and with within-group selection being substantially and continuously debilitated, even a moderately robust degree of selection at the between-group level could have provided leverage sufficient to support genes carried by born altruists—at moderately robust levels. I have not suggested that altruistic genes were likely to have reached the frequencies of genes that made for egoism and nepotism—far from it, unless unbelievably intensive warfare was present. But it would appear that such genes could have been in a position to have reached fixation at levels that were both statistically substantial and significant with respect to social behavior.

CONCLUSIONS

The problem of explaining human social behavior on the basis of natural selection remains formidable, and the same explanatory challenge arises when other animals become generous toward non-kin.[11] Through their combined efforts Trivers (1971), Campbell (1972), Wilson (1978), Alexander (1987), Simon (1990), Tooby and Cosmides (1992), and Boyd and Richerson (1992) have developed a plausible and elegant set of arguments to show how human degrees of altruistic cooperation could be socially enforced or socially facilitated in a species that is assumed by nature to be selfishly nepotistic, and nothing more. However, some of these explanations become quite complicated by the time human group life is fully accounted for. Indeed, for our highly distinctive species, with its complex and often highly "generic" modes of cooperation among nonrelatives, an individual-selectionist paradigm that provides great parsimony through its simplifying assumptions and elegant models simply does not perform optimally.

I began with three distinct hypotheses. If all three of the proposed paths for support of altruistic behavior were operative at a robust level, there would be little problem with the argument that humans are innately disposed to be generous with nonrelatives. While the possible combined effect may be of interest, I have made the arguments separately for several reasons. One is that each "path" could, in theory, operate quite independently, and another is that each path needs to be tested independently as available evidence permits. Still another is that present theory and evidence would appear to favor the third, "egalitarian syndrome" hypothesis. For that reason, I have kept it disentangled from the other two hypotheses.

Although "pleiotropic" subsidies are surely the most difficult to model, the empirical evidence pointing to extensions of nepotistic helping to nonkin beneficiaries is pervasive—not only for humans, but for a number of other well-studied, highly social species (e.g., Goodall 1986). One problem is that accidental side-effects should not be invoked if evolutionary explanation can be effected straightforwardly, in terms of environments affecting gene pools. Also I must emphasize that the "pleiotropic-subsidy" hypothesis merely explains the support that generous *behavior* is receiving at the level of phenotype. The genes that make this support possible remain selfishly nepotistic in their selection, as opposed to altruistic (Boehm 1999b). But a pleiotropic-subsidy model does provide an explanation that is independent of the free-rider problem, and it has the potential for being combined with a group-selection model (see Boehm 1981; Simon 1990).

The warfare hypothesis does provide direct support for altruistic genes, and it is readily combined with the egalitarian syndrome hypothesis. In reexamining Paleolithic conditions and putting them together with what is known about extant foragers and their political and "territorial" behaviors, I have argued that political conflict (including small-scale raiding for vengeance or natural resources) should not be arbitrarily ruled out in considering the evolution of human degrees of genetic altruism. It is conceivable that group conflict making for elevated extinction rates at the between-group level could have preceded the rise of egalitarianism, but there is a dearth of relevant archaeological evidence before the Mesolithic. In any event, without sustained and substantial free-rider suppression it seems questionable that any degree of "warfare," by itself, could have supported a significant rise in the frequencies of altruistic genes. However, after the egalitarian syndrome and moralistic suppression of free riding arrived, intergroup conflict could have further empowered between-group selection in its support of altruistic genes.[12]

The main argument stands by itself, even though possible interactions with the other two hypotheses have been suggested. It concerns human moral communities, the egalitarian syndrome they made possible, and, crucially, the effective policing of opportunistic free riders that takes place in such communities. Empirical support for various phases of the argument has depended upon what data hunter-gatherer ethnographers choose to quantify, and at times I have had to rely on anecdotes, or even to guess about data that remain in field notebooks. However, we do know that mobile foragers live an intensely moral community life, that they make common decisions that are likely to vary between groups, and that they are very good at identifying and punishing (or otherwise manipulating) social deviants, including serious bullies and cheaters. The result was a prehistoric social environment that made genetic selection of altruistic traits more likely than has been assumed.

This main hypothesis places between-group selection in a position to support substantial fixation of altruistic genes in human gene pools. This would have been the case so long as actuarially sophisticated social control obliged born free riders to behave similarly to the born altruists. I have argued that this was the case, and that there have been at least several thousand generations for gene pools to be modified accordingly. This would be true even if egalitarianism arrived only, say, 75,000 years ago. This conclusion may require further work, especially in terms of mathematical modeling, but it definitely could be of importance for understanding human nature.

Today our nature can be expected to reflect, fairly precisely, conditions that obtained in the Upper Paleolithic (see Tiger and Fox 1971). Such conditions include the levels at which natural selection operated (Boehm 1997b), and on that basis humans should be extremely "selfish" and strongly "nepotistic," but at least moderately "altruistic." The reason that moderately altruistic humans are so good at cooperating is that as groups we readily understand how to stimulate cooperation by manipulating the ambivalent social potential of our own species. Those acting as altruistically oriented moral enforcers can identify and manipulate free-rider types precisely because they possess the same free-riding tendencies themselves—if in smaller measure. Conversely, the reason that many born free riders are so amenable to being steered in the direction of altruistic behavior is that they, too, harbor *altruistic* tendencies—in smaller measure. As potential deviants they are encouraged by social "carrots" to act on the prosocial side of their nature, but bands also can become menacing if encouragement fails: they quickly turn to punishment. Thus a potential deviant free rider is influenced simultaneously by prosocial messages and by the threat of the communal stick.

What is fascinating is that all of these highly ambivalent and essentially selfish beings, some genetically more prone to free riding than others, manage to fashion a social milieu in which major carrots coexist with the obvious major sticks, and in which intensive cooperation takes place not only among family members and close relatives, but among people who are unrelated. Whereas altruism probably constitutes no more than a substantial minority component in human nature, it would appear that with powerful, focused, and actuarially sophisticated moral and cultural reinforcement, a moderate dosage of altruistic genes has taken our unusual species a long ways.

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NOTES

1. A better technical term would have been something like "group-helpful" gene (see Boehm 1979), for the biologist's terminology quickly becomes confusing (see Smuts, this issue). In everyday parlance, when I sacrificially help my offspring, or some other relative, or an unrelated member of my group, and am giving without expectation of an equalized return, all of the above may be called "altruism." However, biologists must set aside the first two as "nepotism" because the selection bases of "nepotism" and "altruism" are very different. I shall make it clear by context when I am speaking of "altruistic genes" or "altruistic traits" in a technical, natural-selection context, and when I am speaking of helpful, self-sacrificial, empathetic generosity in the normal, psychological sense of the word "altruism."
2. Genetic group selection is defined technically by Wade (1978) and Wilson and Sober (1994). Basically, *cultural* group selection involves individuals copying other individuals (see Boyd and Richerson 1985; Soltis et al. 1995), and there seems to be no close mechanical analogy at the level of genes.
3. This contrast is not as stark as might appear, for kin groups may also be treated, theoretically, as units of between-group selection (see Sober and Wilson 1998). While Potts (1998) has discussed the selection role of various "lineage" types in the Paleolithic, here the focus is on bands *as multifamily units* because the theoretical issue is the problem of altruism. In fact, most hunter-gatherer bands can be analyzed either as kin groups or as clusters of unrelated families for they have both characteristics. Either type of analysis can be useful.
4. In terms of gene selection taking place at the between-group level, a great deal of intergroup movement of families or exchange of women, whether by marriage or capture or long-term visits, would raise problems that must be taken into account in mathematical modeling.
5. If bonobos are more derived than chimpanzees (Wrangham and Peterson 1996; see also Stanford 1998), then it seems likely that our mutual ancestor engaged in perimeter defense more intensive than what is reported for bonobos (Kano 1992), where casualties are not recorded so far. But in any event, further observation of *Pan paniscus* is needed.
6. If females became scarce because of occasional polygamy, or preferential female infanticide, or high risks to males during the hunt, then females could have been a special additional source of competition between groups.
7. Where bands lived (or migrated) in nexuslike clusters (see Heintz 1972), and pursued territorial goals at that level, the maximum group vehicles would have been several times larger but the mutual isolation of groups also could have been much greater because families tend not to transfer from one internally friendly band cluster to another.
8. I am aware of no published data that would help to disconfirm this hypothesis. However, relevant data may exist in the field notes of hunter-gatherer ethnographers.
9. Unfortunately, according to Dirks (1980), Turnbull's (1972) rich but impressionistic description of recently transplanted and supposedly "agriculturalized" Ik foragers, with their apparently pervasive lack of sharing, has to be discounted heavily.

10. This is so even though average individual reproductive life spans probably were being extended by the egalitarian cooperation that was possible in bands.

11. The implied contrast between humans and other animals should not be taken as being absolute with respect to the three proposed paths to altruism. The "pleiotropic subsidy" hypothesis may have relevance for other species that engage in prolonged offspring nurturance—particularly if they are highly labile behaviorally, and if, in fact, reliance on social (as opposed to hard-wired) kin-recognition mechanisms (see Fox 1989) can serve as an obstacle to natural selection because of bonding with non-kin. With respect to the amplification of between-group variation in other species, hamadryas baboons (Kummer 1971) live in multifamily groups that make and enact their foraging decisions as groups, and this could be boosting the power of *between*-group selection whenever the strategies of different troops tend to vary significantly (see Boehm 1978). The same can be said of adjacent gorilla harems, whose basic foraging strategies are dominated by silverbacks. There is also the issue of reducing variation *within* the group. Species that are innately prepared to have less dominance hierarchy (see Vehrencamp 1983) would exhibit less variation at this level, as would innately hierarchical species whose coalition patterns tend to sharply reduce the phenotypic advantages of high-ranking individuals (e.g., de Waal 1996; Kano 1992; see also Boehm 1999b; Goodall 1986). Furthermore, a rare species that exhibited high rates of politically activated decimation because of intergroup conflict (e.g., Goodall 1986; Nishida 1979) would also be boosting the power of between-group selection. However, unless there are mechanisms that serve to *drastically* reduce free riding, as humans accomplish on an intentional basis, these effects on variation might not affect the levels of altruistic genes sufficiently to influence behavior in significant ways.

12. There is another hypothesis I must mention briefly, with respect to the human *potential* for warfare. Elsewhere (Boehm 1999b), I have argued that after the egalitarian syndrome appeared, with at least a few thousand generations to do its work, the increasing representation of altruistic genes in human gene pools began to make intensive, genocidal warfare more likely. Warfare of this type is an unusually self-sacrificial type of cooperative activity, one likely to have arisen (with proper environmental stimulation and cultural backup) only after the requisite altruistic genes were present. The emergence of *intensive* warfare in the Mesolithic (possibly earlier) could have been linked preadaptively to the prior appearance of the egalitarian syndrome. With time, this syndrome helped to prepare human nature not only for warfare, but for various other types of "extreme generosity" associated with ultrasociality.

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