

INTERACTIONS OF CULTURE AND NATURAL SELECTION
IN THE UPPER PALEOLITHIC

Christopher Boehm
Director, the Jane Goodall Research Center
Department of Anthropology
University of Southern California

INTERACTIONS OF CULTURE AND NATURAL SELECTION IN THE UPPER PALEOLITHIC

INTRODUCTION

Interactions between natural selection and cultural processes have been studied for several decades, with increasing emphasis on specific case studies. The modern pioneer was Donald T. Campbell (1965b, 1972, 1975), who likened the self-organizing side of cultural process to blind variation-and-selective-retention in biological process. Subsequently Boyd and Richerson (1982, 1985) defined these self-organizing processes in terms of conformist transmission mechanics (see also Cavalli-Sforza and Feldman 1984; Boyd and Richerson 1991), while Boehm (1978, 1991, 1996) has emphasized the intentional side of cultural selection by focusing on individual and group decisions. Finally, Durham (1976, 1982, 1991) has broadly integrated the field of human gene-culture coevolution, using case studies that take account of both self-organizing and intentionally guided processes.

Here I offer some hypotheses about one major phase of this interactive process, a phase that involved the emergence of the first human moral communities. The hypothesis is that over time, a moral approach to keeping social order began to impact on the very process of natural selection, and that this changed human nature in ways that influenced morality as we know it today. To understand this sequence of events, it is necessary to start at the beginning, with an ancestral ape.

CLADISTICS

A four-species cladistic model will be set up, by which any behavior that is shared by all four African-based hominoids (humans, chimpanzees, gorillas, and bonobos) can be posited as being present in the earlier hominoid that was ancestral to these species. Wrangham (1987) developed a tentative behavioral model of this ancestor, and the modeling was highly conservative because it is so unlikely that convergent evolution could cause all four species to arrive at a new behavior that was absent ancestrally. The coevolutionary analysis in this chapter will be anchored by a rather complete description of the four-species Common Ancestor's behavioral repertoire.

I shall be borrowing from a prior analysis (Boehm 1999b), in which four-species cladistic modeling was used to identify preadaptations useful to the evolutionary emergence of political egalitarianism. Preadaptation involves putting old traits to new uses as environments change, so we are interested not only in how the Common Ancestor was likely to have behaved in its actual environments but also in any behavioral potential that could have been stimulated by new environments. Because of this interest in preadaptive potential, in triangulating to ancestral traits I shall consider not only how the four descendent species behave in nature, but in how three of them, the African great apes, behave in novel environments, notably, in captivity.

ANCESTRAL USE OF RESOURCES

It is agreed that the Common Ancestor was a quadrupedal arboreal ape whose main diet was fruit or leaves (see Foley 1995; Tattersall 1993). However, we will be guessing at many other aspects of the subsistence pattern because the four descendent hominoids vary considerably. Human hunter-gatherers depend substantially on flesh in their diet (Kelly

1995); chimpanzees do so to a moderate but highly significant degree (Stanford 1999); and bonobos do a certain amount of hunting (Kano 1992; Wrangham and Peterson 1996); by contrast, gorillas at best pick up the occasional insect (Fossey 1983). Thus, whereas the more recent Human-*Pan* ancestor (see Wrangham and Peterson 1996; Stanford 1998, 2000) was likely to have been a hunter, the earlier Common Ancestor must be left as indeterminate as to whether meat was included in its diet. We simply cannot tell, whether gorillas lost a compelling interest in animal fat and protein, or whether the other three species developed it after gorillas split off.

Common Ancestral foraging groups were closed, with definite social boundaries (Wrangham 1987), and they probably were smallish, ranging from about a dozen to a hundred or so. Human hunters, chimpanzees, and bonobos live in fission-fusion groups, with continual formation of ad hoc subgroups whose size is determined by foraging conditions, whereas gorillas essentially stay together as a single harem unit (see Boehm 1999b). Thus, the Common Ancestor lived in smallish closed groups that moved around foraging for food, while the Human-*Pan* Ancestor can be further specified as having a fission-fusion social structure.

Territorially, the picture is less clear. Human foragers often engage in defense of natural resources (see Ember 1978; Dyson-Hudson and Smith 1978; Cashdan 1983), as do chimpanzees (Goodall 1979; Nishida 1979). Bonobos show some tendencies in this direction (Kano 1992; Wrangham and Peterson 1996), but because gorillas are not observed to compete for natural resources the Common Ancestor must be left as a question mark, territorially.

A POLITICAL PORTRAIT OF THE COMMON ANCESTOR

When Wrangham (1987) developed the four-species Common-Ancestral behavioral model, relatively little was known about bonobos or lowland gorillas, and he surveyed only accounts of natural behavior. Although he identified several basic patterns of social behavior that included closed groups and stalking and killing of conspecifics by males, coalition behaviors were taken as being dubious or absent in females and males, and one fundamental type of social behavior was not evaluated at all. This was social dominance hierarchy (see Tiger and Fox 1971), with the status rivalry that underlies it.

In retrospect, this descriptive hiatus is understandable. Even though chimpanzees, gorillas, and bonobos clearly live in hierarchies, in 1987 the case of humans was rather ambiguous. Hunter-gatherers, the appropriate humans for comparison, were considered by many scholars to be just naturally egalitarian, as opposed to innately hierarchical. This was the case even though a few scholars such as Fried (1967) and Service (1962, 1975) had noted that hierarchy was more muted than absent (see also Flanagan 1989), and more recently others had been implying (Lee 1979; Woodburn 1979) or asserting (Boehm 1982, 1984; Woodburn 1982) that egalitarianism involved the use of coercive subordinate force to keep down would-be individual dominators.

In 1993, building on other relevant work (e.g., Cashdan 1980; Fried 1967; Gardner 1991; Service 1962; Woodburn 1982), I advanced a formal hypothesis: egalitarian hunter-gatherers and the tribesmen who followed them were just as hierarchically inclined as humans living in chiefdoms or states, but, because subordinates were firmly (and dominantly) in control, this gave a false impression of “non-hierarchy.” For long, this

impression had been reinforced by a scholarly propensity to find human precursors who were “just naturally equal,” and there was initial resistance to this interpretation (e.g., commentaries in Boehm 1993; Erdal and Whiten 1994, 1996; see also Wiessner 1998). However, the general hypothesis now appears to be widely accepted (e.g., Knauft 1994; Wiessner 1996; commentaries in Boehm 2000). I shall therefore amplify the scope of Wrangham’s appraisal by assuming humans to be just as involved with status rivalry, and just as hierarchically inclined, as the other three apes (Boehm 1999b). This makes the Common Ancestor hierarchical, as well, and this feature is critical to the arguments to come because dominance and punishment are intrinsic to social control.

The Common Ancestral political model I am building here is based not only on a new interpretation of hunter-gatherer politics as being heavily involved with their own brand of hierarchical behavior (Boehm 1993), but on more recent findings from primatological studies in the wild, and on abundant and fascinating data on behavior in captivity.

Furthermore, whereas Wrangham’s model was basically “social,” the model I present here is specifically sociopolitical: I am interested in the uses of individual and collective power in group life because they played a critical role in the evolutionary development of morality.

The Common Ancestor engaged in political coalition behavior (see Boehm 1999b), which is very prominent in humans and wild and captive chimpanzees (de Waal 1982; Goodall 1986), is noteworthy in wild and captive bonobos, and definitely is seen with gorillas.

Bonobo females form coalitions that enable them to compete with males in certain behavioral contexts such as feeding (Kano 1992; Stanford 1999), while bonobo males tend

to hang together politically when two communities meet (see Wrangham and Peterson 1996). In multimale harems, male gorillas form coalitions to defend the harem, while in captivity females have been seen to unite and drive away a new silverback when they already had a younger male who was leading them (de Waal 1982). Because all four extant species form male or female coalitions that are larger than dyadic partnerships, this behavioral potential was present ancestrally and therefore was present in the human line from the beginning.

CONFLICT RESOLUTION AS A KEY PREADAPTATION

Another behavior present in all four hominoids is pacifying-interventions in conflicts (Boehm 1999b). Humans in bands at least try to intervene triadically, though they are not very successful (Furer-Haimendorf 1967); chimpanzee males and females of higher rank intervene in a pacifying mode (Boehm 1994; de Waal 1982), and the same is true of silverback gorillas regulating their harem females (Fossey 1983). Bonobos are less well studied in this respect, but similar patterns have been observed.

This innate aversiveness to conflict within the group, along with the active tendency to manipulate protagonists in the direction of pacification, was an important pre-adaptation for moral behavior. Indeed, people in hunting bands dislike conflict, and behaviors they single out for negative sanctioning are mostly ones that lead to conflict (Boehm 1982, 1999b). Furthermore, de Waal's (1989) work on peacemaking among primates (see also Cords 1997; de Waal 1996; Aureli and de Waal 2000) suggests that the Common Ancestor also intervened *after* conflicts, to assist protagonists in calming down and reconciling. This behavior, seen also in humans, testifies further to the fact that the

Common Ancestor was highly conflict-averse.

A HYPOTHESIS ON MORAL ORIGINS

An evolutionary definition of morality is behavioral rather than philosophical (Boehm 2000). We must focus on the fact that all human groups reach explicit agreements about behaviors that need, respectively, to be encouraged or discouraged, and that in the face of antisocial behaviors they will take steps to strongly manipulate the deviants involved. Because many types of deviance are aggressive, or dangerous, and because measures taken against a deviant may be resisted by his allies, it is necessary for groups to reach unanimity when they decide to sanction him. Indeed, if a minority or bare majority were to sanction a deviant, and then his supporters were to step in to defend him, this would throw the group into factionalized conflict far more disruptive than the original deviance (see Boehm 1999a, 2000).

Elsewhere, in a series of publications (e.g., Boehm 1999b) I have been building a scenario for the evolutionary development of morality sometime after the human line diverged from the *Pan* line. This Common Ancestral model provides a maximally conservative assessment of key behavioral potentials that were available to subsequent moral evolution: closed hierarchical social groups, formation of larger-than-dyadic political coalitions, and aversiveness to conflict within the group with active interventions by individuals bent on pacification. As of about seven million years ago, these were the ancient raw materials out of which human moral communities grew.

Obviously, there is more involved with morality than formation of large coalitions of

group members who share negative feelings toward individuals whose provocative behaviors they wish to discourage. Whether groups could even agree about which behaviors were deviant or laudable without symbolic communication is open to speculation, but De Waal (1996) does provide one anecdote in which this seems to be taking place as captive chimpanzees use a single vocal signal, combined with body language, to express their common hostility toward an individual who is misbehaving.

There are two ways in which the linguistic aspect of culture does seem to be critical to the formation of hunter-gatherer moral communities as we know them. People do need to communicate symbolically if they are to agree on values and behavioral standards that make up a *well-specified* moral code. Perhaps more important, in a fission-fusion group such as a band, in order to identify deviants and agree to collectively manipulate their behavior, highly specific referential communication is needed. This is because many of the individually predatory behaviors that are regularly condemned by foragers can take place in isolation, so victims must be able to report to the group and the group must be able to evaluate the facts. In this context, gossiping seems to be not only an inveterate social fixture that Dunbar (1996) has likened to social grooming, but a generalized means of deviance detection and deviance evaluation that is crucial to social control as we know it today (Boehm 1999b).

A HYPOTHESIS ON THE FIRST SANCTIONING

Without a Common-Ancestral model, the question of what transgressions earlier humans first defined to be “sins” would be a matter of total speculation. However, if we juxtapose the behaviors that extant hunter-gatherers invariably condemn and sanction with the

behavioral repertoire of the Common Ancestor, there is one (and only one) ancestral behavior that is suggestive as a precursor. Ancestrally, *group* action was not taken about deception, a rare great ape behavior in any event, nor was it taken against theft, nor against incest as a favorite candidate of many theorists, nor against rape. The only ancestral behavior that is directly suggestive of egalitarian hunter-gatherer moral proscription and sanctioning is the work of subordinate coalitions to reduce the power of those above them, i.e., to reduce the bullying power of alpha-male types.

All four extant hominoids not only show aversion to being dominated (Boehm 1999b), but actively form small coalitions to neutralize such domination. Moralistic humans can carry this much further, to the point that all nomadic foragers remain egalitarian. This means that they treat one another as equals, do not permit bullying behavior that could eventually intimidate an entire group, and even refuse to countenance strong leadership (Boehm 1993). This definitive reversal of the usual dominance process is possible only because entire communities are able to do the necessary political work: every band is a moral community that insists on egalitarianism---and it can unite unanimously to suppress its bullies. This phase of hunter-gatherer moral behavior definitely is presaged in the Common Ancestor.

There was an ecological development, that could have been important in triggering the systematic social control of dangerous deviants by their groups. Humans began to rely increasingly upon large game, and, as this was taking place over a long span of evolutionary time, their brains were becoming larger and their actuarial intelligence (Boehm 1999c) was becoming quite formidable. There were recurrent junctures at which

protracted and very heavy reliance upon game was all but dictated by changing meteorological conditions (see Potts 1996), just as is seen with today's Inuit peoples (e.g., Balikci 1970), and at such times it would have become perceptually obvious that a smoothly operating and equitable system for sharing out large-game meat would provide better nutrition and better survival chances for all band members. We call this "variance reduction" (Smith and Boyd 1990; Kelly 1995), and hunter-gatherers fully appreciate the averaging principles involved (Boehm 1999c).

By contrast, *pre-moral* humans surely had a markedly hierarchical social system, and therefore were unlikely to engage in efficiently equalized sharing. Indeed, although chimpanzees as dedicated hunters do share meat, it is high-ranking males that get the lion's share (Stanford 1999). Humans are able to share meat quite evenly because social customs and moral rules manipulate the behavior of individuals, and prevent better hunters or bullies from taking disproportionate shares (Kelly 1995).

EARLY MORAL COMMUNITIES

Once prehistoric bands had learned to work together to suppress alpha tendencies and facilitate the sharing of game, they had arrived at a culturally-based methodology that was applicable to other social problems. As cultural animals who also communicated symbolically, referentially, and with displacement, they were now in a position to create rules in other spheres aside from bullying, and to sanction those rules by means of punishment or social pressure. Included, surely, were rules against cheating, lying, theft, and probably a variety of sex crimes as locally defined. The latter might well have included behaviors that interfered with pair bonding---assuming that the institution of marriage was

being supported by earlier moral communities.

In this way, people were able to anticipate and sanction behaviors likely to lead to conflict.

When such pre-emption didn't work, we may assume that, like extant foragers, they did their best to resolve ongoing conflicts through third party interventions, be these individual or collective. Although nomadic foragers today keep their leaders too powerless to be very effective in mediating serious conflicts, as groups they are able to manage earlier stages of conflicts fairly effectively, for instance, by staging duels that dissipate negative energies (see Hoebel 1954).

AN IMPORTANT RESIDUAL PROBLEM

The Common Ancestor was innately prepared to be competitively dominant, and equally good at submitting. It also knew how to join forces politically, and to be punitive in working its will, at both individual and group levels. When groups are pushed to the point of moral outrage, punitive social control becomes prominent in all human societies; thus, all that was necessary, to have moral communities, was the ability to set standards of conduct with respect to behaviors deemed to be antisocial, to identify and communicate about deviants, and to apply punitive collective force in manipulating or eliminating deviants, be the force psychological or physical.

Aside from punitive sanctioning, there is a side of present day moral communities that is far more difficult to explain in terms of biologically-based precursors. Nomadic hunters go beyond negatively setting up prohibitions and manipulating malefactors by force or threat thereof, for they also issue moralizing calls for altruism and cooperation (Campbell 1972,

1975). Unlike coercive manipulations, these prosocial messages have no precedents in the Common Ancestor. The tangible rewards include praise, deference, and respect for the virtuous, and while this positive sanctioning works in tandem with negative sanctioning, generally it is less reported. This is because it tends to be subtle compared with an enraged community's deciding to criticize, ostracize, expel, or even execute a serious offender.

One explanation for this prosocial side of moral development, with its calls for willing and generous cooperation, might be that humans have acquired some evolved propensities to altruism that were not present in the Common Ancestor. At the end of the chapter I shall return to positive sanctioning, to see how this less appreciated side of moral life fits with the gene-culture coevolutionary scenario I am developing.

THE TRANSITION TO MORALITY

I have proposed that important prerequisites for moral behavior were present pre-adaptively in the Common Ancestor, at the level of genetic dispositions to dominance, submission, coalition formation, conflict intervention, and tension-reduction after conflicts. A subsequent development, not found in the three African apes, was tool use after this capacity led to invention of hunting weapons suitable for killing conspecifics. This had an equalizing effect on males because projectiles such as spears or clubs could kill at a distance, and could be used effectively by men who were less physically powerful (Boehm 1999b). These developments helped to set the stage for political egalitarianism, as the first moral accomplishment of our species.

It certainly is possible that morality and political egalitarianism developed very gradually, through gene-culture evolution, but it is not easy to imagine what the earlier stages of moral behavior might have been. It seems at least equally possible that morally-based egalitarianism was invented rather quickly, with language and the invention of effective hunting weapons as preadaptations that made sudden, planned, and decisive political rebellions relatively safe for the subordinates. If morally-based egalitarianism did arrive as an abrupt (and therefore culturally-based) change in political format, it is easy to suggest how this new way of doing things socially and politically could have spread through intentional cultural selection (see Boehm 1978, 1982).

Hunter-gatherers tend to have social intercourse with their neighbors, and with symbolic communication knowledge of newly egalitarian bands would have been quickly available to members of bands still dominated by alpha types. Thus, even a single successful subordinate rebellion would have made for a demonstration effect, with at least one perceptually obvious benefit---the emergence of personal autonomy for all the family heads in the band. The equalized sharing of large game would have been attractive, as well, in case the two were invented simultaneously. In either event, the potential for rapid cultural diffusion would have been great, and the frequent long-range migrations forced on most Paleolithic humans by changing climatic cycles (Potts 1996; see also Boehm 1999c) would have greatly assisted the diffusion process.

COULD MORALITY HAVE AFFECTED SELECTION MECHANICS?

Based on the best available information and methodology, I have proposed a set of interlocking hypotheses to provide an idea of how a crucial event in human evolution took

place, and how it was motivated. The rise of morality is of interest not only because having morals is unique in the animal world, but because moral communities have such special “extragenetic” ways of inducing behavioral uniformity and are so adept at promoting cooperation. In the remainder of this chapter, I shall explore both the influence of Upper Paleolithic human moral communities upon natural selection process, and the impact of natural selection on later developments in the field of social control.

The hypothesis is that the advent of egalitarian moral communities affected levels of selection in ways that favored retention of altruistic traits, and that definitive moralistic control of free-riders enabled this type of selection to proceed fairly robustly (see Boehm 1997). The first issue is whether moral communities arrived early enough for human gene pools to be significantly changed on this basis.

All of the ingredients for morally-based egalitarianism, including language (Deacon 1997; Lieberman 1997), were available with the appearance of Anatomically Modern Humans. If morality appeared 100,000 years ago, that would provide 4000 generations of natural selection under its special cultural influence. According to E. O. Wilson (1978), one thousand generations would be easily enough for a major trait to evolve, so there is no problem with this chronology. However, to bring needed conservatism to a necessarily speculative task, it is better to place the origin of morality at the point when human cultures began to show elaborate evidence of symbolic thought, as other cultural inventions exploded. This brings us to 40,000 to 30,000 years before the present, with the advent of incised lunar calendars, cave painting, and more complex regional elaborations

of stone (and bone) tool technology (see Marshak 1992). This would still allow a little more than the 1000 generations that Wilson suggests may be needed.

So if moralistic egalitarianism had some influence on natural selection as this changed human nature, there appears to have been time for natural selection to have done its work--even if moral communities arrived relatively late in the Anatomically Modern career.

EFFECTS OF THE EGALITARIAN SYNDROME

The prehistoric egalitarian syndrome (see Boehm 1997; Mithen 1990) involved communities in which the heads of households (male or female) morally defined themselves as equals, carefully controlled leadership so it remained weak, and therefore made their decisions by discussing common problems as equals and trying to find a consensus (see also Boehm 1996). As nomads the main type of decision they had to make was where their band would migrate when local resources were used up, or otherwise became scarce. They tried hard to reach a consensus because otherwise the band would have to fragment, and people might find themselves living in groups too small for effective variance reduction. This means that people cooperated in making decisions because they needed to stay together and cooperate in sharing sporadically acquired large game meat.

The overall result was a morally-based system by which two commodities were always shared within the band. One was political power, which in effect was shared among families: household heads were equalized in terms of having both personal autonomy in decision making, and freedom from being physically or psychologically coerced by others with alpha tendencies. The other commodity was large game, which basically was shared

out on an equal basis to every family in the band just as is done so regularly today. In all likelihood, possession of mates also was subject to some significant equalization, as a side-effect of having power and meat equally distributed. The morally-backed institution of stable monogamous/polygamous pair-bonding (marriage) may have arisen in this context (see Boehm 2000).

These behaviors, all implemented by morality, could have had profound effects on natural selection process (Boehm 1997; see also Boehm 1999a, 1999b, 1999c, 2000). First, by eliminating selfish bullying behavior by alphas differences of mating opportunity and of food quantity and quality were significantly reduced within bands. The result: a drastic reduction in individual phenotypic variation within bands, and therefore a weakening of the selection forces that work against altruism. This reduction took place within bands that, as with extant foraging nomads (see Kelly 1995), surely were composed of a mix of related and unrelated families.

In addition, as an effect of making migration decisions collectively, variance in basic subsistence strategies among families of a band was drastically reduced in comparison with each family's being on its own. At the within-band level, this further reduced phenotypic variation among individuals or families. In tandem, these two behavior patterns significantly debilitated within-group phenotypic variation, even though selection taking place within groups remained a very powerful force because extinction rates for individuals were not changed.

In addition, at the between-group level of selection variation was being enhanced. Because bands usually decided to migrate as units, their subsistence strategies were likely to differ

at the band level because each decision was based on a particular concatenation of individuals whose information and manner of processing it were prone to differ. This was particularly the case when ecological stress obliged people to innovate or try risky alternatives, and it was precisely in times of stress that natural selection was likely to operate more powerfully on individuals and groups. For instance, one band might survive a local drought fairly well by investing their last energy in migrating to an area of possible rainfall, whereas a neighboring band might be seriously decimated because it chose to stay in place and wait it out. The next time around, in an unpredictable environment the advantage might go the other way. It was in this manner that varying strategies among bands amplified phenotypic variation at the between-group level of selection (Boehm 1997). Porous boundaries between bands (see Palmer et al. 1998) did not pose a fatal obstacle to this type of selection process (Wilson and Sober 1994; see also Sober and Wilson 1998), and with band composition ranging from just a few dozen to perhaps a hundred persons, the small size of the average units (see Dunbar 1996) was appropriate for some group selection to take place (see Wade 1978). Thus, cooperation among the related and unrelated families living in prehistoric bands could have led to some modest---yet behaviorally significant---gene selection at the between-group level.

Today, human bands are very good at cooperation. One must question whether this collaboration has some direct foundation in terms of altruistic genes (see Wilson 1975), or whether somehow it is accomplished by sociobiologically-defined individuals whose motives are basically selfish and at best nepotistic (e.g., Alexander 1987; Trivers 1971; Wilson 1978). This second viewpoint enjoys wide currency. However even though a great

deal of ingenuity has gone into modeling ways in which selfishness (modified only by nepotism) could result in cooperation among nonkin, for humans this position essentially seems to defy common sense.

In reading the hunter-gatherer literature, my impression is that cooperation is, in fact, likely to be individually ambivalent, and that therefore it seems to require some serious backup from social control. However, one must not ignore the positive side of the ambivalence: this could be based on moderate tendencies to altruism. I emphasize this not only because cooperation often proceeds rather smoothly, but because so often people appear to enjoy engaging in this process, and because, more basically, individuals seem to internalize the prosocial messages that are given in hunting bands. We shall return to this issue later.

Some of our greatest scientific achievements do go against common sense, as with the general theory of relativity or physics. In this context, it is tempting to promote a tough-minded kind of sociobiological approach that defies common sense by reducing all helpfulness and cooperation either to selfishness, to assistance to closer kin, or to very carefully metered reciprocity. However, I think it is scientifically useful to give group selection a chance, as a controversial theory whose further development has been inhibited by sociobiological biases that require further scrutiny.

Along with extinction rates, it is phenotypic variation that drives natural selection at both individual and group levels. In terms of selection mechanics, I have shown that an egalitarian syndrome influences phenotypic variation in ways that would remain quite transparent to theorists who adhered to the sociobiological habit of doing their modeling

at the level of genotype---rather than at the level of phenotype. This widespread practice does work well with nonmoral species, but it is risky with one that is capable of decisive social control (e.g., Boyd and Richerson 1992). With drastic reduction of within-group variation, and with at least a modest increase of between-group variation, these changes at the level of phenotype provide some important food for thought with respect to group selection possibilities.

With moderate group selection in force, minimally genes that were selectively neutral at the individual level but useful to groups (see Wilson 1980) would have had a chance of being retained in human gene pools. Here, I have in mind aspects of Upper Paleolithic cooperation that involved individual contributions that were either cost-free in the first place, or were being evenly reciprocated over time (see Trivers 1971). However, for three decades it has been individually-costly *altruistic* genes that have preoccupied evolutionary biologists, and for their selection there is not only the problem of the lopsided division of labor between within-group and between-group selection, but the formidable obstacle of free-riders (see Hamilton 1964; Williams 1966).

With respect to free-riders, elsewhere I have made an assessment of the ways in which hunter-gatherers deal with attempts to cheat on systems of cooperation and sharing (Boehm 1999b, 1999c). I shall summarize my findings, but first let me emphasize that on the ground, normal types of sharing among *unrelated* families within a band are far from being “automatic” and free of contention.

Indeed, the process of sharing out meat often is tainted by elements of selfishness, and resentment, and in compensation there are a variety of morally-backed cultural institutions

that facilitate sharing. Best known are customs that transfer ownership of large carcasses from the proud and predictably arrogant hunters who acquired them to others who are expected to distribute the meat evenhandedly (e.g., Lee 1979). Even with this morally-based cultural antidote in place, tensions associated with meat-sharing are, in fact, widespread (e.g., Blurton-Jones 1984; Peterson 1993), and the ethnographic record (see Kelly 1995) contains information about occasional sharp quarrels, and significant attempts to cheat, and, if rarely, serious punishment of cheaters by the rest of the band. This is suggestive not only of free-riding attempts---but of free-rider control (Boehm 1999c).

Elsewhere (Boehm 1999c), I have predicted that vigilance about the sharing process (see Erdal and Whiten 1994) will become militant, rather than relatively relaxed, under two sets of circumstances. One is when meat becomes scarce, as under conditions of drought or when the migration patterns of prey become less predictable. There is very little ethnographic data on extant foragers who are experiencing serious stress, but other actuarial accomplishments of hunter-gatherers (see Boehm 1999a) suggest that they are easily sophisticated enough to police free-riding behavior much more carefully during times of scarcity.

The second set of circumstances involves “normal times,” when basically the meat supply should be adequate to group needs. If numbers of free loaders were to rise to such high levels that these parasites were making just a few hunters do all the work, or were significantly reducing meat intake for the group, this too would be an easily recognized problem. In looking at hunter-gatherer ethnographies, it is clear that under normal circumstances bands occasionally do have an individual who is tempted to take a free ride

and manages to do so---for instance, by pretending to be lame when there is hunting to be done. With meat being far from scarce, and with suspicion in this direction, the usual reaction is resentment but no active intervention by the group. However, I know of no accounts of bands in which a sizable number of individuals are suspected of this type of strategy. My prediction is that social tolerance of suspected free-riders decreases either when scarcities arise, or when numbers of “suspects” rise to a level that could be affecting the diet of others. In a band of thirty or forty persons, this number will not be high.

So hunter-gatherers, while not obsessive in their free-rider suppression, damp this type of behavior strategically and effectively, through social control. In doing so, they make very modest individual investments in collective acts of social control that can be very costly to the culprit reproductively (see Wilson and Kniffen 1999), and do this with the most force precisely when their predicted losses will be most significant. This means that even though free-riding is not totally controlled, it is controlled decisively at times when it counts reproductively. This is far from the serious exploitation by free-riders that was modeled by Williams (1966).

By combining changes to levels of selection with effective elimination of free-rider effects, we have a formula for significant group selection of altruistic genes. This process falls within the sociobiological rules set forth by Wilson (1975), but I must leave it to those who build mathematical models of genetic selection process to weigh these factors in a more precise manner. For starters, I feel strongly that it must be phenotype, and not genotype, that is modeled. It also will be necessary to look closely at the demographic dynamics of bands as group vehicles of selection that have “porous” boundaries (see

Wilson and Sober 1994), and also to consider their size. It would be necessary, also, to search the ethnographic literature carefully and discern any patterns of splitting and re-formation of hunting bands of the type that Wade (1978) has discussed from the standpoint of laboratory experiments on insects.

In addition, in working with specific case studies it will be necessary to approximate the changes in the relative strengths of between-group and within-group selection, and, with respect to a given altruistic trait, to calculate the amount of individual cost and the amount of group benefit (see Bowles in press) and enter these into the equation. However, as a cultural anthropologist I have at least roughed out a research program for the evolutionarily open-minded. What we have, here, are conditions that favor at least some moderate selection at the between-group level---selection that could support group-beneficial altruistic traits. It was morality, of course, that made it possible to manipulate behavioral phenotype so definitively.

Aside from favoring altruistic traits, the arrival of egalitarian moral communities surely had other effects on the natural selection of behavioral dispositions. On the basis of inclusive fitness, it seems likely that humans evolved to be more sensitive to group opinion (see Waddington 1960; Campbell 1975; Boyd and Richerson 1985). In my opinion, they also evolved to use their individual dominance more cooperatively, by acting aggressively as groups to reduce the reproductive advantages of bullies, cheats, and other predatory deviants. After at least a thousand generations of living in moral communities it is clear that these changes came far from making today's foragers deviance-free, or from turning them into a nonhierarchical species---that is, an innately egalitarian species in

Vehrencamp's (1983) sense. Hunter-gatherers today still encounter problems with self-aggrandizing selfish upstarts, and encounter them quite predictably in spite of an ethos that strongly supports egalitarianism and altruism. What takes place in socially stratified chiefdoms and nations, where social hierarchy is morally countenanced, further demonstrates a hierarchical nature at work (Knauff 1991).

WHAT ABOUT DIRECT COMPETITION BETWEEN GROUPS?

Developing a better individual capacity for collaborating aggressively against deviants within the group brought significant relative fitness benefits to the cooperating moralists, who now suffered far fewer reproductive losses to internal aggressors or cheats. As this individual capacity for aggressive collaboration was increased by natural selection, the enhancement had one probable side effect. This same capacity can be useful to groups when differences arise *between* them, and they decide to fight. If the scale and intensity of warfare has risen in earlier or recent times, and in the face of grossly inadequate Paleolithic evidence (see Keeley 1996) there is at least a suggestive trend that starts in the Mesolithic, this may have been in part because moral communities pre-adapted us for warfare. The specific hypothesis would be that as individuals became better adapted to operate as large, assertive moral coalitions in their local communities, a generalized capacity to cooperate in sizable aggressive groups would have been enhanced. This would have lowered the threshold of environmental stimulation needed to produce warfare.

If moral communities and the egalitarian syndrome made possible even some modest selection of altruistic genes, this, too, could have contributed to the human potential for warfare. This would be true only of intensive warfare, of the type that involves two large

groups fighting it out. In contrast to small-scale raiding, in which useful net reproductive gains are derived from cautious, individualistic forays in search of booty, large-scale, intensive armed conflict involves individual patriotic self-sacrifice (see Boehm 1999a; Campbell 1975).

Intensive warfare patterns are, in fact, endemic among many tribal-agriculturalist peoples (e.g., Meggitt 1977; see also Soltis, Boyd and Richerson 1993), and some hunter-gatherers engage in them, as well (see Ember 1978). The wonders of modern warfare at the state level are well-known, of course, and our capacity to engage in such cooperative, high-risk behavior, while it stems in large part from social control, may well be enhanced by prehistoric developments involving natural selection. These involved not only individual participation in cooperatively aggressive efforts to control deviants, mentioned above, but also hunting cooperation in small groups which pre-adapted humans to cooperate within small military units (see Richerson and Boyd 1999). The natural selection of group-beneficial altruistic traits (Boehm 1999a) could have been important, as well.

FURTHER EVIDENCE OF ALTRUISM

To summarize, once morality arrived in conjunction with political equality, the egalitarian syndrome could have had profound effects on natural selection process because play was given to group selection forces at the same time that free-riding was drastically suppressed. Even though extinction rates were not affected, changes in phenotypic variation provided conditions conducive to between-group selection.

At the level of selection mechanics, I believe these arguments to be both logical and plausible. But another type of less direct evidence supports this same hypothesis. This involves the division of labor between negative and positive types of moral manipulation, as these are seen in hunter-gatherer and other moral communities. The hypothesis is that the first moral communities relied exclusively on negative sanctioning, and that positive sanctioning arrived only after human nature acquired an altruistic component.

Members of the earliest moral communities agreed on behaviors they did not like, communicated among themselves as they kept track of deviants, and combined forces to discourage deviant behavior or eliminate serious troublemakers from their groups.

Precursors in the Common Ancestor included a capacity for dominant aggression and a capacity for coalition formation, which in combination made it possible for a group to manipulate or kill any of its members. This punitive side of social control has been well-recognized since Durkheim (1933) first emphasized it, and more generally the term “social sanctioning” seems to carry a negative connotation of forceful manipulation or punishment (see Boehm 2000).

This negative type of social reinforcement seems quite consistent with a sociobiological definition of human nature as the product of selection by inclusive fitness:

selfish/nepotistic individuals, devoid of altruism, perceive a common threat to their personal welfare in the form of individual deviance, and unite to deal with it. At the level of individuals, such cooperation is reproductively rewarded because each person shares a major fitness dividend that comes from getting rid of bullies within the group, and because individual risks and energy spent in collective sanctioning are modest. The deviant loses,

and the rule-enforcing citizens share the net profit. Negative sanctioning of this type would seem to be adequate to the task of cutting down political upstarts and maintaining an egalitarian order, and it can be hypothesized that early moral communities operated in this way. The same aggressive techniques could have been applied in controlling other types of predators within the band, and in policing the equalized sharing of large game.

If we move up to the present, what we see is a continuation of this punitive approach, but also what might be called “positive sanctioning.” Positive moral manipulations involve not only giving praise and respect to individuals who behave themselves, but explicit calls for cooperation and generosity (Campbell 1975). While the negative side of social sanctioning has definite precursors in the Common Ancestor, there are no such precursors for positive sanctioning. It seems likely, therefore, that the positive emphasis developed later.

There are two questions that I wish to explore here. First, is a wholly selfish species likely to come up with calls for generosity and cooperation when it already has at its disposal some very effective negative means of reinforcement? Second, are members of a wholly selfish species likely to be *responsive* to such positively-phrased messages?

By “wholly selfish” I refer to a species whose genotype is shaped solely by within-group selection, or inclusive fitness. It is *conceivable* that a wholly selfish species, one that understands the individual dividends that come from cooperation, might consider adding use of carrots to their successful use of sticks, to make cooperation work still better. This cannot be ruled out. However, even a modest element of altruism in human nature would make positive reinforcement far more likely to work, for in a multi-family band even an ambivalently altruistic individual is more likely to respond to a social message that calls for

generous contributions to group efforts. By the same token, an ambivalently altruistic being is more likely to come up with such prosocial messages in the first place, than is a wholly selfish being.

One must keep in mind not only that the evolved altruistic component in human nature is likely to be quite modest, but also that at the level of phenotype feelings of generosity toward nonkin are being heavily amplified by socialization of children in prosocial directions (see Goody 1992), and by social rewards that stimulate generous cooperation in adults. This results in the internalization of prosocial values.

The result is not perfectly motivated cooperation, but effective and usually willing collaboration that invariably reduces variance in meat supply when large game is being acquired sporadically. On one hand, hunter-gatherers do show evidence of ambivalence about sharing their large game. On the other hand, basically the job of variance reduction is accomplished quite efficiently (see Kelly 1995)---in spite of occasional complaints and squabbles.

In this context, internalization of values that favor generosity and cooperation can be quite strong. Indeed, the tendency to share meat when others (outside the family) request it seems often to be all but automatic, and Kelly (1995) provides an anecdote in which the hunter-gatherer sharing ethic is so well-internalized that to deny such a request is virtually unthinkable.

It is of interest that socially-instigated calls for generosity and cooperation, the ones identified by Campbell (1965a, 1972) and found in all six early human civilizations

(Campbell 1975), seem to be echoed in every type of human society. There is no way to prove that individuals who were entirely “selfish” sociobiologically couldn’t have brilliantly come up with such proclamations as manipulative devices, acting purely from Machiavellian motives. But these calls for generosity and willing cooperation are more logically explained if we cede to human nature a modicum of altruism that is being heavily amplified by cultural conditioning.

If this scenario is correct, then the first human moral communities were likely to have dealt in negative reinforcement only: power plays by large, morally-aggressive coalitions were the name of the game. However, as the egalitarian syndrome prevailed over hundreds and hundreds of generations, and altruistic traits were subject to moderate positive selection at the between-group level, human nature was being modified. Once altruistic traits were in place, and were strong enough to make a difference behaviorally, moral life acquired a new, positive component that we see in all human moral systems today.

SUMMARY

In considering interactions of culture and natural selection in the Upper Paleolithic, I have hypothesized that there were a number of genotypically well-prepared precursor behaviors that preadapted our Common Ancestor for the evolutionary emergence of moral communities. As a cultural invention, the acquisition of lethal hunting weapons also made a contribution to this development. The result was the egalitarian syndrome, which was possible only with moral communities that were judgmental and capable of collective sanctioning that was guided by human intentions (Boehm 1999b).

With moral communities, a distinctive new type of behavior had appeared in a mammalian species, in the form of deliberate collectivized social control. At first such control was likely to have been based on threat or use of force, and therefore it was punitive. Nothing more was needed, to produce the egalitarian syndrome that rearranged the division of labor between between-group and within-group selection, and saw the effective curbing of free-riders through social control.

I have suggested that punitive sanctioning was complemented, later on, by positive moral manipulations, and that this new development was likely to have depended upon addition of altruistic tendencies to human nature, tendencies that became strongly reinforced by socialization and group opinion. The final result was a group in which positive and negative types of social reinforcement worked in tandem, and both types of manipulation supported cooperation as a consciously directed human activity.

With respect to issues of coevolution, the scenario I have developed involves natural selection with cultural processes in several ways. First, selection at the biological level set in place the precursors to moral behavior that were conservatively identified in the Common Ancestor. Next, it would appear that egalitarian bands appeared as a product of intentional cultural invention, with subordinates realizing that by standing together they could become individually autonomous. This process could have been protracted, or quite rapid. Next, the resulting egalitarian syndrome profoundly affected natural selection processes, giving significant play to group selection. Finally, evolved altruistic tendencies began to influence moral behavior, providing a positive cast to sanctioning that

complemented---but did not replace---the negative orientation of earlier moral communities.

These hypotheses are never likely to be developed to a degree that outright falsification is likely. However, their importance for defining the human condition justifies their being considered on the basis of relative plausibility. As a cultural anthropologist I have not attempted to create mathematical models to test the important hypothesis about group selection, but hopefully the scenario I have developed may inspire others in this direction. I expect that it may be possible to create realistic models of multi-family hunting bands, taking into account their size, their considerable instability, the ways in which they grow or are decimated, the ways in which they fission, and the ways in which new bands are formed. This would be helpful in further evaluating the relative plausibility of the group-selection arguments I have developed.

ACKNOWLEDGMENTS

I wish to thank the Fyssen Foundation for inviting me to the Paris conference on which this book is based, and the Templeton Foundation for making possible three years of research on hunter-gatherer conflict resolution. I also wish to thank the H. F. Guggenheim Foundation for two grants that supported research on, respectively, egalitarian behavior of humans and chimpanzee conflict intervention. In addition, a fellowship at the School of American Research in Santa Fe, New Mexico, made it possible to develop some of the newer arguments in this paper. I thank Peter J. Richerson for making comments on the paper.

REFERENCES CITED

- Aureli, F. and de Waal, F. B. M. (eds.) 2000. *Natural Conflict Resolution*. Berkeley: University of California Press.
- Alexander, R. D. 1987. *The Biology of Moral Systems*. New York: Aldine de Gruyter.
- Balikci, A. 1970. *The Netsilik Eskimo*. Prospect Heights, Illinois: Waveland.
- Blurton-Jones, N. G. 1984. A Selfish Origin for Human Food Sharing: Tolerated Theft. *Ethology and Sociobiology* 4:145-147.
- Boehm, C. 1978. Rational Preselection from *Hamadryas* to *Homo Sapiens*: The Place of Decisions in Adaptive Process. *American Anthropologist* 80:265-296.
- Boehm, C. 1982a. A Fresh Outlook on Cultural Selection. *American Anthropologist* 84:105-124.
- Boehm, C. 1982b. The Evolutionary Development of Morality as an Effect of Dominance Behavior and Conflict Interference. *Journal of Social and Biological Sciences* 5:413-422.
- Boehm, C. 1984. Can Hierarchy and Egalitarianism both be Ascribed to the Same Causal Forces? *Politics and the Life Sciences* 1:34-37.
- Boehm, C. 1989. Ambivalence and Compromise in Human Nature. *American Anthropologist* 91:921-939.
- Boehm, C. 1991. Lower-Level Teleology in Biological Evolution: Decision Behavior and Reproductive Success in Two Species. *Cultural Dynamics* 4:115-134.

Boehm, C. 1993. Egalitarian Society and Reverse Dominance Hierarchy. *Current Anthropology* 34:227-254.

Boehm, C. 1994. Pacifying Interventions at Arnhem Zoo and Gombe. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, and P. G. Heltne (eds.), *Chimpanzee Cultures* (pp. 211-226). Cambridge, Mass.: Harvard University Press.

Boehm, C. 1996. Emergency Decisions, Cultural Selection Mechanics, and Group Selection. *Current Anthropology* 37:763-793.

Boehm, C. 1997. Impact of the Human Egalitarian Syndrome on Darwinian Selection Mechanics. *American Naturalist* 150:100-121.

Boehm, C. 1999a. Forager Hierarchies, Innate Dispositions, and the Behavioral Reconstruction of Prehistory. In M. W. Diehl (ed.), *Hierarchies in Action: Cui Bono?* Center for Archaeological Investigations, Occasional Paper No. 27. (pp. 31-58). Carbondale: SIU Press.

Boehm, C. 1999b. *Hierarchy in the Forest*. Cambridge: Harvard University Press.

Boehm, C. 1999c. The Natural Selection of Egalitarian Traits. In C. Boehm (guest editor), *Human Nature*, Special Issue on Group Selection 10:205-252.

Boehm, C. 2000. Group Selection in the Upper Paleolithic. In L. Katz (guest editor), *Journal of Consciousness Studies*, Special Issue on the Evolutionary Origins of Morality 7:1-2:211-215.

Bowles, S. in press. Individual Interactions, Group Conflicts, and the Evolution of Preferences. In S. Durlauf and P. Young, *Social Dynamics*. Cambridge: MIT Press.

Boyd, R. and P. J. Richerson. 1982. Cultural Transmission and the Evolution of Cooperative Behavior. *Human Ecology* 10:325-351.

Boyd, R. and P. J. Richerson 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R. and P. J. Richerson 1991. Culture and Cooperation. In R. A. Hinde and J. Grobel (eds.), *Cooperation and Prosocial Behavior* (pp. 27-48). Cambridge: Cambridge University Press.

Boyd, R. and P. J. Richerson 1992. Punishment Allows the Evolution of Cooperation (or Anything Else) in Sizable Groups. *Ethology and Sociobiology* 13:171-195.

Campbell, D. T. 1965a. Ethnocentric and Other Altruistic Motives. In D. Levine (ed.), *Nebraska Symposium on Motivation* (pp. 283-311). Lincoln: University of Nebraska Press.

Campbell, D. T. 1965b. Variation and Selective Retention in Socio-Cultural Evolution. In H. R. Barringer, B. I. Blanksten, and R. W. Mack (eds.), *Social Change in Developing Areas* (pp. 19-49). Cambridge: Schenkman.

Campbell, D. T. 1972. On the Genetics of Altruism and the Counter-Hedonic Component of Human Culture. *Journal of Social Issues* 28:21-37.

Campbell, D. T. 1975. On the Conflicts Between Biological and Social Evolution and Between Psychology and Moral Tradition. *American Psychologist* 30:1103-1126.

Cavalli-Sforza, L. L., and M. W. Feldman 1981. *Cultural Transmission and Evolution: A Quantitative Approach*. Princeton: Princeton University Press.

Cashdan, E. A. 1980. Egalitarianism Among Hunters and Gatherers. *American Anthropologist* 82:116-120.

Cashdan, E. A. 1983. Territoriality among Human Foragers: Ecological Models and an Application to Four Bushman Groups. *Current Anthropology* 24:47-66.

Cords, M. 1997. Friendships, Alliances, Reciprocity and Repair. In D. Byrne and A. Whiten (eds.), *Machiavellian Intelligence II* (pp. 24-49). Cambridge: Cambridge University Press.

Deacon, T. W. 1997. *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: Norton.

Dunbar, R. 1996. *Grooming, Gossip and the Evolution of Language*. London: Faber and Faber.

Durham, W. H. 1976. The Adaptive Significance of Cultural Behavior. *Human Ecology* 4:89-121.

Durham, W. H. 1982 . Interactions of Genetic and Cultural Evolution: Models and Examples. *Human Ecology* 10:289-323.

Durham, W. H. 1991. *Coevolution: Genes, Culture, and Human Diversity*. Stanford: Stanford University Press.

Durkheim, E. 1933. *The Division of Labor in Society*. New York: Free Press.

Dyson-Hudson, R. and E. A. Smith 1978. Human Territoriality: An Ecological Reassessment. *American Anthropologist* 80:21-41.

Ember, C. 1978. Myths about Hunter-Gatherers. *Ethnology* 17:439-448.

Erdal, D. and A. Whiten 1994. On Human Egalitarianism: An Evolutionary Product of Machiavellian Status Escalation? *Current Anthropology* 35:175-184.

Erdal, D. and A. Whiten 1996. Egalitarianism and Machiavellian Intelligence in Human Evolution. In P. Mellars and K. Gibson (eds.), *Modelling the Early Human Mind* (pp. 139-150). Cambridge: MacDonald Institute for Archeological Research.

Flanagan, J. G. 1989. Hierarchy in Simple 'Egalitarian' Societies. *Annual Review of Anthropology* 18:245-266.

Foley, R. 1995. *Humans Before Humanity*. Cambridge, Mass.: Blackwell.

Fossey, D. 1983. *Gorillas in the Mist*. Boston: Houghton-Mifflin.

Fried, M. H. 1967. *The Evolution of Political Society: An Essay in Political Anthropology*. New York: Random House.

von Furer-Haimendorf, C. 1967. *Morals and Merit: A Study of Values and Social Controls in South Asian Societies*. Chicago: University of Chicago Press.

Gardner, P. 1991. Foragers' Pursuit of Individual Autonomy. *Current Anthropology* 32:543-558.

Goodall, J. 1979. Life and death at Gombe. *National Geographic* 155:592-622.

Goodall, J. 1986. *The Chimpanzees of Gombe*. Cambridge, Mass: Harvard University Press.

Goody, E. 1991. The Learning of Prosocial Behavior in Small-Scale Egalitarian Societies: An Anthropological View. In R. A. Hinde and J. Grobel (eds.), *Cooperation and Prosocial Behavior* (pp. 106-128). Cambridge: Cambridge University Press.

Hamilton, W. D. 1964. The Genetical Evolution of Social Behavior I, II. *Journal of Theoretical Biology* 7:1-52.

Hoebel, E. A. 1954. *The Law of Primitive Man: A Study in Comparative Legal Dynamics*. Cambridge, Mass.: Harvard University Press.

Kano, T. 1992. *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford: Stanford University Press.

Keeley, L. H. 1996. *War Before Civilization: The Myth of the Peaceful Savage*. New York: Oxford.

Kelly, R. L. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington: Smithsonian Institution Press.

Knauft, B. B. 1991. Violence and Sociality in Human Evolution. *Current Anthropology* 32:391-428.

Knauft, B. B. 1994. Reply to Erdal and Whiten. *Current Anthropology* 35:181-182.

Lee, R. B. 1979. *The !Kung San: Men, Women, and Work in a Foraging Society*. Cambridge: Cambridge University Press.

Lieberman, P. 1998. *Eve Spoke: Human Language and Human Evolution*. New York: Norton.

Marshak, A. 1992. The Origin of Language: An Anthropological Approach. In J. Wind, E. G. Pulleyblank, E. de Grolier, and B. H. Bichakjian, et. al. (eds.), *Language Origin: A Multidisciplinary Approach* (pp. 421-448). Dordrecht: Kluwer.

Masters, R. D. 1989. *The Nature of Politics*. New Haven: Yale University Press.

Meggitt, M. 1977. *Blood is their Argument*. Palo Alto: Mayfield.

Mithen, S. J. 1990. *Thoughtful Foragers: A Study of Prehistoric Decision Making*. Cambridge: Cambridge University Press.

Nishida, T. 1979. The Social Structure of Chimpanzees of the Mahale Mountains. In D. A. Hamburg and E. R. McCown (eds.), *The Great Apes* (pp. 73-122). Menlo Park, California: Benjamin/Cummings.

Palmer, C. T., B. E. Fredrickson and C. F. Tilly 1998. Categories and Gatherings: Group Selection and the Mythology of Cultural Anthropology. *Ethology and Sociobiology* 18: 291-308.

Peterson, N. 1993. Demand Sharing: Reciprocity and the Pressure for Generosity among Foragers. *American Anthropologist* 95:860-874.

Potts, R. 1996. *Humanity's Descent: The Consequences of Ecological Instability*. New York: Avon.

Richerson, P. J., and R. Boyd 1999. Complex Societies: The Evolutionary Origins of a Crude Superorganism. In C. Boehm (guest editor), *Human Nature, Special Issue on Group Selection* 10: 253-289.

Service, E. R. 1962. *Primitive Social Organization: An Evolutionary Perspective*. New York: Random House.

Service, E. R. 1975. *Origin of the State and Civilization: The Process of Cultural Evolution*. New York: Norton.

Smith, E. A. and R. Boyd 1990. Risk and Reciprocity: Hunter-Gatherer Socioecology and the Problem of Collective Action. In E. A. Cashdan (ed.), *Risk and Uncertainty in Tribal and Peasant Economies* (pp. 167-192). Boulder: Westview.

Sober, E. and D. S. Wilson 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, Mass.: Harvard University Press.

Stanford, C. B. 1998. The Social Behavior of Chimpanzees and Bonobos: Empirical Evidence and Shifting Assumptions. *Current Anthropology* 14:399-420.

Stanford, C. B. 1999. *The Hunting Apes: Meat Eating and the Origins of Human Behavior*. Princeton: Princeton University Press.

Tattersall, I. 1993. *The Human Odyssey: Four Million Years of Human Evolution*. New York: MacMillan.

Tiger, L. and R. Fox 1971. *The Imperial Animal*. New York: Delta.

Trivers, R. L. 1971. The Evolution of Reciprocal Altruism. *Quarterly Review of Biology* 46:35-57.

- Vehrencamp, S. L. 1983. A Model for the Evolution of Despotic versus Egalitarian Societies. *Animal Behavior* 31:667-682.
- de Waal, F. B. M. 1982. *Chimpanzee Politics: Power and Sex Among Apes*. New York: Harper and Row.
- de Waal, F. B. M. 1989. *Peacemaking Among Primates*. Cambridge, Mass.: Harvard University Press.
- de Waal, F. B. M. 1996. *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Cambridge, Mass.: Harvard University Press.
- Waddington, C. H. 1960. *The Ethical Animal*. Chicago: University of Chicago Press.
- Wade, M. J. 1978. A Critical Review of the Models of Group Selection. *Quarterly Review of Biology* 53:101-114.
- Wiessner, P. 1996. Leveling the Hunter: Constraints on the Status Quest in Foraging Societies. In P. Wiessner and W. Schiefenhovel (eds.), *Food and the Status Quest: An Interdisciplinary Perspective* (pp. 171-191). Oxford: Berghahn.
- Wiessner, P. 1998. On Emergency Decisions, Cultural Selection Mechanics, and Group Selection. *Current Anthropology* 39:356-358.
- Williams, G. C. 1966. *Adaptation and Natural Selection: A Critique of some Current Evolutionary Thought*. Princeton: Princeton University Press.
- Wilson, D. S. 1980. *The Natural Selection of Populations and Communities*. Menlo Park: Cummins.
- Wilson, D. S. and K. M. Kniffin 1999. Multilevel Selection and the Social Transformation of Behavior. In C. Boehm (guest editor), *Human Nature, Special Issue on Group Selection* 10:291-310.

Wilson, D. S. and E. Sober 1994. Reintroducing Group Selection to the Human Behavioral Sciences. *Behavioral and Brain Sciences* 17:585-654.

Wilson, E. O. 1975. *Sociobiology: The New Synthesis*. Cambridge: Harvard University Press.

Wilson, E. O. 1978. *On Human Nature*. Cambridge, Mass.: Harvard University Press.

Woodburn, J. 1979. Minimal politics: the political organization of the Hazda of North Tanzania. In W. A. Shack and P. S. Cohen (eds.), *Politics in Leadership: A Comparative Perspective* (pp. 244- 266). Oxford: Clarendon.

Woodburn, J. 1982. Egalitarian Societies. *Man* 17:431-451.

Wrangham, R. 1987. African Apes: The Significance of African Apes for Reconstructing Social Evolution. In W. G. Kinzey (ed.), *The Evolution of Human Behavior: Primate Models* (pp. 51-71). Albany: SUNY Press.

Wrangham, R. and D. Peterson 1996. *Demonic Males: Apes and the Origins of Human Violence*. Boston: Houghton-Mifflin.