

# The Evolution of Human Ultra-sociality

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# 1.0 Introduction

## 1.1 Human sociality in comparative perspective

E.O. Wilson (1975) described humans as one of the four pinnacles of social evolution. The other pinnacles are the colonial invertebrates, the social insects, and the non-human mammals. Wilson separated human sociality from that of the rest of the mammals because, with the exception of the social insect like Naked Mole Rats, only humans have generated societies of a grade of complexity that approaches that of the social insects and colonial invertebrates. In the last few millennia, human societies have even begun to exceed, in numbers of individuals and degree of complexity, the societies of ants, termites, and corals.

Human social complexity is based on quite different principles than the ultra-sociality of any other species. In all other known cases, the constituent individuals of societies are either genetically identical, as in the colonial invertebrates, or closely related, as in the social insects and non-human mammals. In the prototypical social insect colony, elaborate societies are built around a single reproductive queen, who suppresses the reproduction of workers in the colony. The offspring of the queen are siblings that share many genes in common, and they make up the work force of the colony. W.D. Hamilton (1964) argued in his famous pair of papers that worker sterility and relatedness to each other and the queen are fundamental to insect sociality. It is interesting to note (Wilson and Hölldobler 1988) that the phylogenetic rarity of eusociality in insects is in sharp contrast to its ecological ubiquity. Ants and termites are among the most abundant insects, and social bees and wasps are by no means rare. As with other social animals the range and adaptive diversity of the human species has increased, and our population densities have exploded, as our societies have grown more sophisticated. Thus, the cooperation, coordination, and division of labor that characterize ultra-social animals appear to be highly adaptive in many contexts. At the same time, evolutionary processes can rarely overcome the conflicts between individual reproductive success and the cooperation and self-sacrifice required to produce the colony-level benefits that ultra-sociality produces.

Humans are, arguably, a new page in the natural history of animal cooperation (Campbell 1983). Our reproductive biology is similar to the other social mammals. Among our close relatives, the apes and monkeys, genetic relatedness and reciprocal altruism support a diverse array of small-scale societies, but no other spectacular ones. Humans have built extremely complex societies by some mechanism or mechanisms different than any other known highly social species. At the same time, there are remarkable parallels between human and ape social behavior

(deWaal 1982) and material culture (McGrew 1992), not to mention many convergences between humans and other social and tool-using species. Consistent with classical comparative anatomy and modern molecular studies, human behavior is clearly recently derived from ape behavior. There is room for only relatively few modifications of the behavior of the last common ancestor of chimpanzees and humans.

In this chapter, we draw together the results of some of our own theoretical work on the role of the processes of cultural evolution in the evolution of human sociality, the contributions of human sociobiologists, the general comparative data on the form of human societies, and some critical experimental data from psychology to develop a hypothesis about how human ultra-sociality might have arisen by the Darwinian coevolution of culture and genes. We believe that evidence from several independent theoretical and empirical domains support the hypothesis.

## **1.2 The argument in outline**

Our basic claim in this chapter is that cultural evolutionary processes drove the evolution of human ultra-sociality. The cultural transmission of ordinary adaptive information has advantages in the highly variable environments of the Pleistocene, and the hominine line diverged from the last common ape ancestor in developing a massive dependence on adaptive social and technological traditions. Some of these processes have the effect of making group selection *on cultural variation* possible and the use of *cultural cues to structure populations* common. As cultural group selection began to produce primitive patterns of ingroup cooperation and outgroup hostility, human cognitive capacities and emotional responses, presumably coded in large measure by genes, responded to adapt people to living in culturally defined cooperative groups.

Cultural transmission is a little like the haplodiploidy of the social insects. It tweaks the evolutionary process in a way that happens to make the evolution of ultra-sociality possible. It is quite unlike haplodiploidy in that it leaves the genetic system of inheritance itself unaltered. Thus human ultra-sociality arose by adding a cultural system of inheritance to a genetic one that normally supports small-scale societies based on kinship and reciprocity.

Our account is a modernization of Darwin's (1874) argument in Chapters III-V of the *Descent*, where he outlines his theory of the evolution of the psychological basis human ultra-sociality. His account turns on a mixture of what we would call today reciprocity based on foresight of consequences, aided by group selection (see also Alexander 1977, 93 ff.). For the

usual reasons, genetic group selection is likely to be weak in humans (but see Wilson and Sober 1994, and commentators). Group selection on *cultural* variation is a different story.

## **2.0 Kin Selection, Reciprocity, and Punishment In Human Societies**

Most evolutionary biologists believe that all known cases of non-human animal cooperation can be explained by kinship and reciprocity. Both are certainly important in human societies.

Kin selection is fundamental to the evolution of cooperation in many animal societies. Not only is the eusociality of the social insects built upon kinship, but so are the much more modest social systems of the non-human primates. In the case of our closest relatives, the chimpanzee, the core of the social system is sets of related males (Goodall 1986). A population composed of relatively small, relatively exogamous kin groups with limited reproductive suppression of subordinate members of societies is a rather typical pattern for social mammals.

There is little doubt that cooperation with kin is deeply ingrained in human psychology. One excellent body of evidence comes from the seemingly tangential literature on incest avoidance. Westermarck (1894) suggested that there is an innate avoidance of inbreeding. If so, humans must have an innate kin recognition system. The operation of this device is nicely illustrated by the rarity of marriage among Israeli kibbutz age-mates (Shepher 1983) and the poor success of Taiwanese minor marriages (Wolf 1970). In these famous examples, potential husbands and wives are raised in close companionship as children, much as siblings normally are, even though unrelated in fact. Co-resident agemates apparently have an innate algorithm that invokes an mating avoidance mechanism. The kin recognition system fails in the rather unusual circumstances discovered by Shepher and Wolf, but in normal families will function properly as an incest avoidance mechanism.

Daly and Wilson (1988) explore a useful set of data on patterns of homicide. Family members, living in close proximity, have the maximum opportunity to kill one another, and family homicides are a large fraction of the total. Nevertheless, there is a striking tendency for consanguineal relatives to refrain from killing each other, compared to affinal family members. For example, child abuses and child murders are very disproportionately committed by step-parents. The homicide data, like that from incest avoidance, strongly suggest that humans have deep-seated psychological mechanisms for kin recognition and for kin appropriate behavior, as predicted by Hamilton's theory of inclusive fitness. One famous example of human altruism argued

to contradict the theory, Polynesian adoption practices, turns out to strongly support it (Silk, 1980). Kin altruism no doubt has deep roots in the vertebrate order, and human examples of nepotistic behavior can be multiplied at will.

Trivers (1971) described a mechanism whereby long-continued interactions between partners might lead to the development of sufficient trust in reciprocation of acts of aid to make such acts routine. Axelrod and Hamilton (1981) analyzed the case of pairwise interactions of players of prisoner's dilemma in their important contribution to the theory of reciprocity. In their model, the interaction has a given probability of continuing for another turn. In this situation, it is easy for strategies like "tit-for tat," ("cooperate on the first round of the game, and then do whatever your partners did on the previous round of the game") to evolve. If two players of this strategy meet, they cooperate from the first. If tit-for-tat players play against an unconditional non-cooperator, they receive the worst possible sucker's payoff on the first round of the game, but are only victimized once. If payoffs to cooperation are relatively high and games go on for many rounds, then selection can prevent unconditional defectors from invading a population of tit-for-tat strategists.

Most important for our purposes here, Alexander (1987) has proposed that Axelrod's and Hamilton's result can be extended to very large societies by what he calls indirect reciprocity. If one of us helps you, you may help some third person who in turn helps the other of us. Rather than being restricted to pair-wise interactions, perhaps reciprocity can encourage cooperation among large, diffuse networks of reciprocators. Primatologists (Byrne and Witten 1988; Dunbar 1992; Kummer et al., in press) provide some support for this idea in the form of what is called the "Social Intelligence Hypothesis." Perhaps primate encephalization is generally an adaptation to managing more complex societies, and humans are merely the most extreme case. Dunbar's data suggest that brain size is correlated with group size in non-human primates. Intuitively, the trouble with supposing that intelligence alone can increase cooperation is that smart individuals can compute selfish advantage and learn sophisticated deceptive tactics just as readily as they can compute their enlightened self interest via cooperation. Intelligence may be necessary to manage human cooperation, but is it sufficient to produce it?

We have studied mathematical models of the effects of group size on the evolution of strategies like tit-for tat. In one series of models, we considered unstructured groups in which all individuals in the group simultaneously played repeated turns of prisoner's dilemma (Boyd and Richerson 1988). We generalized the idea of tit-for-tat to large groups by studying rules of the

form "cooperate if  $k$  out of the other  $n$  individuals cooperated on the last iteration of the game." The tit-for-tat results do not generalize to large groups. As group size increases, it rapidly gets very hard to get reciprocity to increase when rare in a population dominated by unconditional defection. This makes sense. In a situation where interacting groups are of size ten and your rule is cooperate if 5 others do, it is highly improbable the five others with the same rule will be in any given group when rare. Alexander's idea involves indirect reciprocity flows along fairly stable networks (what goes around eventually comes around). Adding a ring structure to groups to organize reciprocity in larger groups helps, but not much (Boyd and Richerson 1989).

It is often suggested that punishment of rule-breakers plays an important role in the maintenance of cooperation. The defection of tit-for-tat strategists when their partners defect is a kind of punishment, but in large groups it is very inefficient since it leads to the breakdown of cooperation for cooperators as well as defectors. It should be much more efficacious to punish defectors by discriminating retribution and go on cooperating with other cooperative individuals. We used the repeated prisoner dilemma system to model how punishment might evolve (Boyd and Richerson 1992). Each round of the game is divided into two parts. In the first part individuals in a group of size  $n$  either cooperate or defect. In the second stage of the round some strategies will, at some cost, punish those who defected in the first part of the round. The results of this theoretical investigation suggest that a division of labor can arise in which a few punishers can induce a larger number of reluctant cooperators to cooperate. At equilibrium, under a range of conditions, a group tends to have one punisher, just the number needed to induce cooperation in most groups. This result is reminiscent of the famous bigman political systems of New Guinea, and common in tribal societies elsewhere. We need not imagine that "punishers" are brutal thugs dictating cooperation by physical coercion. "Bigmen" may be, as Eibl-Eibesfeldt remarked at the conference, prosocial leaders who pay the costs of persuading and cajoling to induce cooperation from others, with perhaps the distant threat of physical harm.

Punishment suggests the possibility of the evolution of "moralistic" strategies in which punishers punish reluctant cooperators not only for defecting themselves, but also if they do not punish others who fail to cooperate and even those who fail to punish those that don't punish. Such strategies can certainly induce cooperation, but they can also make any arbitrary behavior an ESS that happens to become the target of a moralistic strategy.

This effect is in turn only an extreme example of the way games of coordination arise in models of cooperation. In games of coordination, it is best to do whatever everyone else is doing.

You may hate daylight savings time, but it is quite inconvenient to arrange life around standard time when everyone else is using daylight savings. As models of cooperation become more complex, there are typically many ESSs, introducing a coordination effect. Moralistic strategies can potentially make even absurd things, like wearing neckties to work, evolutionarily stable. Cultural evolution is perhaps rapid enough to evolve to different coordination equilibria in different local populations, leading to group selection among societies with different equilibria. It is likely that genetically determined variation in coordination equilibria exists only at the species level, making interdemographic group selection on the basis of different coordination equilibria unlikely.

There is no doubt that humans are capable of using rules about appropriate behavior in partners as a basis for social decisions and actions. Cosmides (1989) conducted a series of experiments to test the hypothesis that at least one of the kinds of problems that people evolved to solve are those that involve social contracts. She supposed that human cognition includes the rule "if you take the benefit, then you must pay the cost." Of many simple rules that humans might use in social or more general decision-making this one is uniquely suited to detecting defection in games like repeated prisoners dilemma. She then tested subjects ability to solve a logical problem when couched as a social contract compared to their ability to solve it couched as some simple non-social problem. For example the rule "if a man eats cassava, he has a tattoo on his face" can be framed as a social rule (only men who have undergone the painful ritual of tattooing can eat cassava) or as a mere contingent empirical fact (tribes that eat cassava also happen to tattoo). Framed as a cheater detection problem success rates were in excess of 70%, while less than 25% solved the problem in its empirical guise. Cosmides interprets these results to mean that people have an innate decision-making module devoted to detecting cheaters on social contracts. Whatever one might think of the innate interpretation of the experiment, it would certainly appear that humans are very efficient decision-makers when it comes to detecting defectors on a social contracts.

In addition to recognizing cheaters in social games, people seem psychologically prepared to exact retribution. Daly and Wilson (1988) report high rates of spousal homicide in some modern communities. Suspicion of infidelity and sexual rivalry are very common motives for murder. Knauft (1987) notes that in small-scale communities lacking any formal authority, murder is quite common. In the absence of a satisfactory rule of law (which poor people can't afford, and some simple societies don't have) individuals are certainly capable of costly acts of punishment. Of course, the ultimate threat of physical coercion backs up formal law.

The capacity of people to behave as reluctant cooperators is strikingly demonstrated in experimental settings such as those constructed by Milgram (1974) and Nuttin and Beckers (1975). In one of Nuttin and Beckers' experiments, Belgian college students (male) were asked by Beckers (an attractive young woman experimenter) to give a speech in *favor* of a hated exam system, to which they were subjected. A strenuous protest movement *against* the system was supported by virtually all students. In the most extreme experimental condition used, all 11 students assigned to experimental treatment requesting students to give a television speech favoring the exam system complied with Beckers' request for cooperation. 22 fellow students were asked how many students would comply with such a request, the majority thought less than 5%, and the most cynical guessed 30%!

### **3.0 Kin Selection, Reciprocity and Punishment Are Not Enough**

There is no doubt that kinship, reciprocity and punishment--family, friends and righteous anger--are important components of human social life. There is little doubt that they account for the eusociality of insects and the small-scale cooperation of non-human primates. However, it is hard to imagine how to make a case for these processes, unaided, creating human ultra-sociality.

The comparative evidence strongly suggests that the conventional mechanisms aren't sufficient. If kin selection, reciprocity, and punishment were sufficient to create ultra-sociality in local populations with open mating and without reproductive suppression of workers, then ultra-sociality ought to be common in our relatives, given its ecological success in our case. Unusual adaptations suggest unusual environments or unusually evolutionary processes.

The common theoretical problem that afflicts all three processes is that they all inherently favor small groups, absent special mechanisms like sterile worker castes. Kin altruism should favor the most closely related individuals differentially. Sibships and even first or second cousinships are composed of relatively few people. All else equal, it is much easier to organize reciprocal cooperation in smaller groups than in larger ones. Even if cooperation in large units gets started somehow, the relative ease of organizing nepotistic cooperation and small cabals of reciprocators will tend to subvert larger scale organizations. It would seem that socially intelligent individuals might organize many pairwise reciprocal arrangements, but not engage in much indirect reciprocity.

Punishment by a leader has natural limits in the ability of an individual to monitor and coerce reluctant cooperators. Also, the cooperation produced by leaders creates a public good for

all participants. If leaders can control group size in their own interest, they are not likely to select the group size that maximizes overall benefits. If the marginal cost of having more than a few individuals in the group exceeds the benefits, leaders will keep groups small. In fact, in the classic iterated prisoner's dilemma model to which we added punishment, the per capita benefits do not increase as a function of group size, and potential leaders would prefer to be loners and have to coerce no one. The asocial heroes that Clint Eastwood often plays in films illustrate this result. His characters can coerce cooperation from whole towns, but they only do so when circumstances make exit impossible. At the other extreme, it is easy to imagine situations in which punishment is cheap, and in which punishers can reward themselves disproportionately from the fruits of cooperation. Leaders would then be motivated to assemble a large number of exploitable retainers. In this situation, coerced individuals will exit if they possibly can. What is lacking in the punishment systems, and in related moralistic strategies, is any obvious internal mechanism to regulate them in the group interest, even approximately. The comparative evidence (Eibl-Eibesfeldt 1989: 297 ff.) is not supportive of the idea that coercion can generate ultra-sociality. Coercion and deference to coercion are very widespread in animal societies in the form of dominance hierarchies and similar principles of social organization. Dominant animals sometimes act as prosocial leaders. Human dominance behavior shows many continuities with animal dominance, and if dominance behavior alone could build large societies, they ought to be common in other social animals.

Our hypothesis, then, is that these conventional mechanisms for the evolution of cooperation in humans act quite strongly, but only to favor the same small-scale cooperation that they do in other mammals. They are a major source of *conflict* in human societies (Campbell, 1983). Process of cultural group selection build large scale ultra-social institutions which very frequently compete with kinship and friendship for the loyalties of people. This conflict has no easy resolution because the culture-driven institutions and psychological mechanisms that support ultra-sociality have been added in on top of a mating system, family system, and face to face reciprocity system that derives directly from life in small primate troops, as zoologists have noted (Harcourt 1992).

Micro-sociological data seem to support the conflict hypothesis. Predatory crime, fraud, embezzlement, anti-trust violations and the like, when they are cooperative at all, are typically organized on a small scale. Pairs of robbers may engage in their enterprises with *some* confidence that they have solved the prisoners dilemma problem.. Larger scale criminal enterprises, like the

Mafia and the Colombian drug cartels, resemble legal ultra-social institutions. They use principles of recruitment like ethnicity and ritualistic resocialization to extend their scale of organization far beyond what a single kin group or band of close friends can accomplish. Olson (1982) gives evidence that the postwar economic success of the countries defeated in W.W.II can be explained as the result of the temporary absence of small-scale organizations exploiting large-scale institutions. In Germany and Japan, the pre-war totalitarian regimes destroyed or co-opted many small-scale social organizations. Then, denazification and demilitarization destroyed the organizations created by the totalitarian regimes. The constitutions imposed on the two countries by the Allies reconstructed national scale organizations, and for some period of time these operated free of the influence of a multitude of small-scale interest groups. The economies of the Allied victors grew more slowly because "special interest" organizations remained intact, demanding expensive and inefficient subsidies and other aid at the expense of the nation as a whole.

#### **4.0 Genetic Group Selection Implausible**

Several prominent modern Darwinians [W.D. Hamilton (1975), E.O. Wilson (1975: 561-2), R.D. Alexander (1987: 169), and Eibl-Eibesfeldt (1982)] have given serious consideration to group selection as a force *in the special case* of human ultra-sociality. They are impressed, as we are, by the organization of human populations into units which engage in sustained, lethal combat with other groups, not to mention other forms of cooperation. The trouble with a straightforward group selection hypothesis is our mating system. We do not build up concentrations of intra-demic relatedness like social insects, and few demic boundaries are without considerable intermarriage. Moreover, the details of human combat are more lethal to the hypothesis of genetic group selection than to the human participants. For some of the most violent groups among simple societies, wife capture is one of the main motives for raids on neighbors. In precontact New Guinea, warfare typically results in the social breakup of a defeated group, and the dispersal of its members to other groups where the defeated have bonds of friendship and kinship (Soltis et al. 1995). Pastoralists in Eurasia generated complex intermarrying confederations across ethnic lines to the extent that it takes considerable detective work to be reasonably certain that groups like Attila's Huns were mainly a Turkic group (Maenchen-Helfen 1973). The human groups that compete are demographically very open, and violent conflict increases migration rates. It is hard to see how genetic differences can be maintained in the face of such migration rates.

## **5.0 Cultural Evolutionary Processes and Ultra-sociality**

### **5.1 Introduction**

Are there cultural evolutionary processes that can support the evolution of norms and sentiments that permit people to live in large cooperative groups, even in the teeth of small-scale loyalties based on kinship and reciprocity? Humans are unique in the scale of their use of learning from others as a mode of adaptation. Cultural transmission is like genetic transmission in many respects, although the differences are just as important (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). We are also unique among vertebrates in the scale of our social cooperation, the degree to which social groups are marked by symbolic means, and apparently unique among all animals in the mode by which we construct them. Thus, it is worth pursuing the hypothesis that the association of culture and cooperation is not accidental. We think that there is good evidence that cultural evolutionary processes did play a role loosely analogous to haplodiploidy and reproductive suppression of workers in engendering human ultra-social institutions.

### **5.2 Cooperation and cultural group selection**

#### **5.2.1 Theoretical models**

Intuitively, group selection on culturally transmitted variation is more plausible than in the genetic case because of differences in the way culture is transmitted. One such difference is that humans may survey several individuals in the course of acquiring a cultural trait. We can have more than two cultural “parents.” In variable environments with migration between subpopulations, there are liable to be many erroneous ideas introduced into the population by outsiders whose behavior is appropriate for a different environment. We can expect that the adaptive forces--even natural selection--to act on culture to keep advantageous traits in high frequency so long as the amount of migration is not overwhelming. Theoretical models show that using a conformist transmission rule of the form “when in Rome, do as the Romans do” is advantageous in this circumstance. Individuals benefit by using the information about the commonness or rarity of a cultural trait to bias their adoption choice. This transmission rule in turn has the effect of reducing variation within populations and protecting between-population difference. Even with fairly substantial migration rates and relatively weak conformity, the

differences between groups is maintained in the models (Boyd and Richerson 1985: Ch. 7). Cultural group selection meets the test of theoretical plausibility, a test that most evolutionary biologists believe genetic group selection flunks.

In addition to between-group differences stabilized by conformity, games of coordination, the coordination element in many games of cooperation, and moralistic punishment all lead to multiple evolutionarily stable equilibria. If cultural evolution is generally more rapid than genetic evolution, and there is reason to assume that this is one of the basic adaptive advantages of learning by imitation (Boyd and Richerson 1985: Ch. 4), then cultural metapopulations may find more alternative equilibria than metapopulations without culture, and there will be more variation at the group level on which selection might play.

### **5.2.2 Empirical data**

The cultural group selection hypothesis predicts that social units that are co-socialized should be the groups that cooperate. Some evidence supports this prediction. Otterbein's (1968) cross-cultural study of warfare revealed that societies engaged in internal warfare had small-scale fraternal interest groups composed of related males as the dominant element of social organization. Societies that suppressed internal warfare and conducted mostly external warfare emphasize socialization of warriors into age sets, police societies, or other military institutions that cross-cut units of male relatedness. When the cultural group that is co-socialized is restricted to genetic kinsmen, we recover, approximately, as expected, the pattern predicted by ordinary kin selection theory. When a larger group is the focus of socialization for military virtues, larger scale fighting units emerge.

Elsewhere we have reviewed the psychological evidence that humans actually use conformist rules in cultural transmission. Despite a large literature on conformity, more work is needed on the extent to which we actually use it in cultural acquisition. (Boyd and Richerson 1985, 223-7).

It is also possible to test the empirical plausibility of the cultural group selection process with a direct microevolutionary analysis. Soltis et al., (1995) used information on group extinctions by warfare in Highland New Guinea to provide an estimate of the plausibility and power of group selection. The New Guinea data provide relatively extensive and sophisticated ethnographic accounts for a series of simple tribal societies before contact with colonial powers. Although horticultural rather than hunting and gathering societies, the sorts of processes operative

in Highland New Guinea are roughly similar to those that might have operated on simple societies generally over the long period of time during which human ultra-sociality arose.

To work effectively, cultural group selection by the conformity mechanism requires a number of conditions to be effective. For example, new groups must be formed mainly by the splitting of old groups, not by drawing random samples of migrants to a new group. The former mode of group multiplication preserves variation between groups, whereas the latter destroys it.

Group extinctions due to chronic warfare between village communities are quite common in New Guinea. For the five populations for which quantitative estimates could be derived from the literature, rates ranged from 1.6% to 31.3% per generation. Taking into consideration the quality of the data used in the estimates, the long-term, area wide rate was probably between 10% and 20%. The New Guinea data strongly support the model's assumed group reproduction processes. New groups always arise by the fissioning of existing groups, usually large, successful ones. There is ample evidence for cultural differences between groups, although there is little evidence in Highland New Guinea ethnography documenting differences that persist for long periods of time or that are directly connected to extinctions. Other sets of data do strongly suggest that group differences in competitive ability are common (e.g. Barth 1981; Knauff 1985, 1993).

Taking the New Guinea rates at face value, our calculations suggest that cultural group selection can cause an initially rare, favored institution to become common in about a millennium. This rate is fast on the time scales of genetic macroevolution, and is roughly consistent with rates of evolution of human political institutions under pre-state conditions. The archaeological and linguistic evidence from Western North America, where hunting and gathering subsistence is the rule, suggests that major events causing population displacements did indeed have approximately millennial time scales (Bettinger and Baumhoff 1982). If this process began working sometime back in the Pleistocene, then there will have been some tens of millennia, perhaps as many as a few hundred, for this process to have affected human social cognition by genetic coadaptations to life under group selected cultural adaptations.

We know from simpler cases that cultural evolution can drive a genetic response in cases like the evolution of adult lactose absorption in dairying populations on the millennial time scale (Durham 1991: Ch. 5). If a process like cultural group selection worked over substantial periods of time, and especially if it recruited coercive strategies to effectively punish defectors from social

contracts, it is reasonable to expect that human decision-making strategies should be adapted to life in a prosocial world.

Batson's (1991) experimental studies of the psychology of human altruism provide good evidence that our cognitions and emotions have been molded by some form of group selection. His studies address the structure of motivations that produce helping behavior using laboratory experiments. The experiments were designed to distinguish between an empathy-altruism hypothesis and various forms of covertly egoistic motives for helping behavior. According to the empathy-altruism hypothesis, once a potential helper's empathy for a sufferer is engaged, helping behavior is motivated, at least in measurable part, by a genuinely unselfish desire to actually relieve the victim's suffering. Rational actor theorists propose that instead of a desire to help for its own sake, apparent altruists give aid in the expectation of some form of personal reward. Egoistic hypotheses are numerous. Individuals may help another in need because they seek to gain rewards or avoid punishment. These expected rewards and punishments may be external or internal. That is, people may expect others to give rewards or administer punishments, or it may be a matter of conscience, self-administered rewards and punishments. Expected external rewards or punishments may be material (soldier's pensions) or social (enhanced prestige). Of course, actual human motivations may be complex, and egoistic motivations of several kinds may jointly act with altruistic ones. Batson's question is whether any significant non-egoistic motivation can be demonstrated.

The experiments elicited an empathetic response on the part of some experimental subjects, for example by asking them to take the point of view of the experiment's victim, while non-empathetic controls were asked to view the situation objectively. Then, the experimental conditions were manipulated to control for one or another egoistic motivation and test whether subjects in the empathy condition still willing to provide aid to the experiments victim. For example, one egoistic motivation for aiding a victim might be to relieve one's own suffering at having to watch the victim suffer. To test this possibility, "Elaine," the sham victim in one experiment, was to suffer a series of moderately painful shocks. The experimental subjects were told at the beginning of the sham experiment that Elaine is unusually sensitive to shocks due to a traumatic childhood experience, and finds them exceedingly uncomfortable. The experimenter expresses concern about this, and offers the real subjects the chance to continue the "experiment" in place of Elaine. The shocks will be uncomfortable for them, but not nearly so painful as for Elaine. If helping is motivated by the desire to avoid viewing someone else suffering, Batson

reasoned that allowing the experimental subjects to escape (watch only two trials of the experiment on Elaine instead of all ten) should reduce the tendency to help, whereas if subjects had a genuine desire to help Elaine, even subjects allowed escape should offer to help. In this experiment, difficult escape had a dramatic effect on helping in the low empathy case, raising the proportion helping from about 0.2 to 0.6. In the high empathy condition there was no significant difference in helping; in the easy escape condition the proportion offering to help was 0.9, and in the difficult escape, 0.8. While the egoistic motivation clearly had some effect, the helping in the empathy condition is consistent with the empathy-altruism hypothesis.

Batson even produced evidence that people's desires to aid others go beyond conscience and pride, internal psychological punishments and rewards for helping. In experiments in which the desire to help was aroused and then frustrated by someone else getting to help, an internal reward system would elevate the mood of those who got to help, but not those that did not. Contrary to this hypothesis, subjects who saw help provided, but didn't have to provide it themselves, had the greatest mood increase, and those that were prevented from helping when no one else did had the lowest mood. Once empathy is engaged, people apparently have a genuinely unselfish desire to help.

A skeptic about the effects of group selection does have rejoinders to these experiments. Genuine proximal altruism could be part of a strategy of advertisement of one's willingness to engage in acts helping kin and reciprocal partners, and perhaps be made consistent with some form of the social intelligence hypothesis. However, the cultural group selection hypothesis provides the most natural evolutionary explanation for Batson's results. If cultural groups have long been subject to group selection, then fellow group members ought to engage in empathy-altruism even when kinship is remote and expectations of reciprocity limited. The question is, what arouses our empathy?

### **5.3 Ideology and symbol system evolution: Ingroup marking**

It is a striking feature of human ultra-sociality that groups are explicitly defined and marked by symbolic boundaries. Some of these marks are relatively simple badges such as body ornamentation and dialects. Others are complex ritual systems accompanied by elaborately rationalized ideologies. It is a commonplace that social relations are regulated by norms embedded in a group's sanctified belief system (Rappaport 1979). Even in simple hunting and gathering societies, the groups so marked are rather large, as we already noted. In this section we argue that symbolic cultural marks are potent factors dividing ingroups from outgroups, sharpening the boundaries between social units subject to cultural group selection, and regulating empathy and hence altruism.

#### **5.3.1 Theory**

We have studied models of a processes we term “indirect bias” (Boyd and Richerson 1985: Ch. 8; 1987). In indirect bias, individual imitators use one trait in potential cultural models to weight that individual in the socialization process. Young people picking adult role models on the basis of charm, prestige, power, or whatever is a commonplace example. Once a role model is chosen, youngsters may pick up a number of other ideas, norms, skills, and attitudes without further bias. If any of these other traits happen to correlated with indices of prestige or charm that youngsters are using to choose role models, then the correlated variants will increase in frequency.

The evolution of symbolic, stylistic markers of group boundaries is an interesting special case of cultural evolution under indirect bias. We (Boyd and Richerson 1987) investigated a model of the evolution of “ethnic” markers motivated by these observations. Supposed that there are two episodes of transmission. In the first episode, children learn some neutral marker trait, like a speech dialect, from their parents and other local adults. In the second, they learn a subsistence trait and modify their dialect by selecting among a broader set of adult models. In the first episode there is just blind copying. In the second, models are weighted by both their symbolic trait and their subsistence success. Juvenile imitators prefer models with a dialect like that they learned as children, but also prefer successful models. The broader set of models in the second episode is meant to mimic the effects of cultural diffusion from one environment to another. The question is, in an environment in which the best subsistence strategy is variable from place to place, can a symbolic marker reducing the effect of cultural diffusion of locally maladaptive traits from

neighboring environments arise? The answer is yes. If there is a sharp environmental gradient, a dialect difference will emerge and continue to get more extreme until the degree of cultural isolation is sufficient to allow the population to optimize the mean subsistence behavior. Thus, to the picture of a culturally group selected hominid from the previous section, we can also, in theory, imagine that the boundaries between groups are formally marked by symbol or style changes.

### **5.3.2 Empirical evidence**

Archaeology suggests that the acquisition of a fully symbolic cultural system led to a considerable increase in human adaptive sophistication (Bettinger 1991: 203-8). One notable feature of the human species, increasingly apparent throughout the Pleistocene, is our very wide geographical range. In Europe, stylistic features of culture marking apparent ethnic differences first appear at the Upper Paleolithic Transition, about 35,000 ybp. Upper Paleolithic peoples apparently had more regionally differentiated subsistence strategies and greater population densities than the Middle Paleolithic populations they replaced. Upper Paleolithic peoples also extended the human range into such isolated land areas as Australia and the New World.

There is a fair amount of data on the microevolutionary properties of indirect bias. First, it is highly plausible that people use indirect bias effectively for everyday culture acquisition. This is quite well documented in the applied literature on the diffusion of innovations (Rogers 1983). It also seems that in many societies, culturally defined prestige, which people use as indicators for indirect bias judgments, is correlated with wealth and reproductive success (Irons 1979; Borgerhoff Mulder 1988). As the theory suggests, everyday fitness advantages can be obtained by using indirect bias. Second, ethnographic investigations suggest that the symbolic, stylistic markers in the form of body adornment and the like are used to communicate and negotiate personal and social identities relative to others. Wiessner (1984) makes a strong case for such usage in the Kalahari San. These data, together with the appearance of stylistic artifacts at the Upper Paleolithic Transition, argue that expressive symbolic displays have been part of human strategies for managing cultural transmission, among other problems of social life, for a respectable period. Third, there is also evidence, again Wiessner's (1983) San data is an example, that ethnolinguistic boundaries are symbolically marked, and that stylistic marks of group membership are highly salient. Wiessner collected arrow points from a number of Bushmen groups, including groups unknown to the Kalahari San and in fact ethnically rather different from

them, and asked San men for comments on the distinctive styles. Confronted by points of an unknown style, Kalahari San guess that their makers are very different people from themselves. Within groups, on the other hand, exchange of stylistically familiar beadwork and other valuables is used to build up a notion of the Kalahari San social universe and to build a web of relationships that link people within ethnolinguistic units.

At the proximal psychological level, the “minimal group” experimental system developed by Tajfel (Tajfel et al. 1971) is interesting regarding the cognitive mechanisms involved in the use of symbols to demarcate groups, and the actions people take based on group membership. It is a common finding in social psychological experiments, as in real life, that members of groups favor one another and discriminate against outgroups. The social psychologists in Tajfel’s tradition were interested in separating the effects of group membership *per se* from the personal attachments that form in groups. Turner (1984) contrasts two sorts of hypotheses to explain group oriented behavior. It could be that functional social groups are composed entirely of networks of individuals that are linked by personal ties, objective shared fate, or other individual-centered ties, much as in the social intelligence hypothesis. Groups, on this hypothesis are “some collection of individuals characterized by mutual interpersonal attraction reflecting some degree of interdependence and mutual need-satisfaction.” The contrasting hypothesis is that identity symbols alone are sufficient to induce humans to accept membership in a group, acting positively toward ingroup members and negatively toward outgroups.

In his prototypical experiments, Tajfel, et al. (1971) told subjects that they were participating a test of aesthetic judgment. They were shown pictures of paintings by Klee and Kandinsky, and asked to indicate which they preferred. Then the subjects were divided into two groups, supposedly on the basis of their art preference, but in fact at random. The subject’s task was then to divide a sum of money among members of one’s own group or the other group. Subjects discriminated in favor of the sham ingroup members. The interpretation of these results was that indications of membership, even in a new, externally imposed, and very abstract group, was sufficient to motivate ingroup favoritism on the part of subjects.

Turner *et al.* (1983) were interested an extreme case of categorization generating group-oriented cooperative behaviors. Could such behavior be motivated by an external categorization of a group in which the group was categorized as those everyone, including group members, disliked? Children were shown their picture paired with others and asked to rate the others as liked or disliked. Then children were ostensibly placed in groups by explicitly random criteria, or

on the basis of liking or on the basis of disliking in different treatments. In still other treatments, children were not explicitly placed into groups. Then children had to make private decisions about rewards to allocate to others. Being explicitly assigned to a group had a marked effect, as in the classic Tajfel design. The most striking contrast was that in the ungrouped condition, disliked children favored liked others. However, when they were explicitly grouped as to liked or disliked, disliked subjects, led to believe that they were now members of a group of pariah disliked others, discriminated almost as much as liked-group members in favor of their fellow pariahs (recall classic films like *The Seven Samurai* and *The Dirty Dozen*, where the plot turns on the bonding among a group of initially hostile outcasts). Turner (1984) argues that such experiments show that even shared membership in a group of unattractive others can induce a commitment to the group. Categorization *per se* does have a strong effect, independent of inter-personal bonds.

Other social psychologists have objected that Tajfel and Turner have overemphasized the raw categorization effect in interpreting their experiments. Rabbie (1991) argues that no experimental system implying that people belong to a group can control away people's expectation that the group membership imposed by experimenters implies instrumental interdependence. From an evolutionary point of view, Rabbie's point is well taken; people presumably only react to symbolic badges of group membership because in the evolutionary past they generally signal politically important social units. In the politically complex world outside the lab, where many groupings are abstractly possible, people no doubt attempt to make sensible decisions about which to take seriously in any given circumstance. Nevertheless, it is striking in humans how a rather abstract, large, impersonal, marked groups (Protestant Irish, Serb, Jew, German, etc.) can attract great emotional salience and motivate desperate deeds of great risk to participants. Long periods of relative dormancy seem to leave largely intact the potential emotional power of groups that can plausibly claim deep historic roots. Individual decision-makers must also contend with the awful possibility that an aggressive outgroup may suddenly, for reasons of its own, target one as belonging to a previously weakly relevant group, as has happened recently to Bosnian Muslims.

## **6.0 Conclusion**

A considerable amount of evidence from several domains ranging from comparative natural history to psychology suggests that the processes of cultural evolution permitted group selection on cultural variation and the marking of group boundaries by cultural symbols. Archaeological evidence suggests that symbolic behavior is at least a few tens of thousands of

years old. The hunting and gathering societies under which these processes operated were composed were very small, overlapping with typical primate bands in size. However, ethnographic studies show that the bands themselves are typically quite fluid, and that “tribal” ethnolinguistic units of 500-1500 people (Birdsell 1968) are an important part of the human social adaptation. Hunting and gathering societies of the ethnographic record appear to expend considerable effort to maintain the ethnolinguistic tribe as an institution. Yengoyan (1968) noted that Australian marriage systems were most complex in the arid, sparsely populated interior. He argues that the complex section systems of the interior ensured that people sought mates from geographically great distances, which kept the dispersed tribe a functional demographic and ceremonial unit. In the harsh, variable environment of Central Australia, the ties at the tribe level were used to gain aid in times of emergency. Although tribal politics among hunters and gatherers is usually quite simple, some cooperation at the level of the ethnolinguistic tribe is very common. While kinship, reciprocity, and dominance organize higher primate troops into units as large as hunter-gatherer *bands*, there is in the non-human species no social unit corresponding to the ethnolinguistic *tribe*.

We suppose that the symbolically marked, cooperating ingroup adaptation was based on psychological decision-making system analogous to Chomsky’s view of language as an innate set of algorithmic principles, whose parameters are set culturally by the specific language learned (Pinker 1994: 111-2). The propensity to cooperate with sympathy inspiring ingroup members, and to use symbolic markers to define ingroups, is a like the innate principles of language. The specific markers, size of group(s), and internal structure of the group(s) to which individuals belong are culturally variable parameters that generate a specific functioning instance of the innate propensities. Like innate language structures and adult lactose absorption, the social decision-making principles most likely coevolved as adaptations to an emerging cultural environment in which cooperation within culturally marked groups was becoming important. Success in intergroup competition came to depend upon within-group cooperation; an evolutionary arms race arose. The scale of cooperation-to-compete might escalate until ecological rather than evolutionary constraints bring a halt. Once the barriers of scale imposed by kinship and reciprocity are breached by cultural group selection, it is not clear what the next natural evolutionary limit to scale of cooperation is. This picture squares with experimental evidence such as Batson’s and Tajfel’s that perhaps give us a look at the innate principles of human social action, and it explains how human societies can organize cooperation on a far larger scale than our primate relatives.

It can be objected that the subjects of these experiments already have considerable cultural sophistication when they participate in such experiments. The same objection applies to the experiments such as Cosmides on cheater detection. Fair enough, some human universals likely involve conservative cultural features as well as genetic elements. But it is also true that chimpanzees would not behave in the same way in any of these experiments no matter how hard experimenters tried, nor would our Australopithecine ancestors of 5 million years ago. Even if we cannot yet be sure exactly what the innate principles are that divide us from other apes we can be sure that they exist, as remarkably human-like as chimp behavior is in so many ways.

Human populations grew explosively in the Holocene when the development of food plant production removed previously tight constraints on human densities. With ecological constraints removed, the cooperation-to-compete arms race renewed its progress. Very large, hierarchically organized societies grew up in the agricultural regions of the world. This phase of social evolution is still an ongoing process. The last 10,000 years have witnessed the repeated emergence of ever more powerful societies, but so sign of any perfected equilibrium adaptation.

Complex societies make lavish use of symbolic boundary marking, and are capable of impressive feats of cooperation, such as road nets, irrigation systems, and, unfortunately, armies. The tendency of ethnic identities to retain great importance in even the most modern societies was a surprise to many social scientists (Glazer and Moynihan 1975). But complex societies also require (or at any rate always have had) a substantial degree of organized coercive control. Ethnographically known hunting and gathering societies have only the weakest forms of leadership and little tendency for leaders to be able to lead lives of privilege at the expense of followers. Human social instincts are certainly not adapted to live in societies numbering in the millions organized by elites that establish a great social distance between themselves and ordinary citizens. The means by which ancient social instincts and modern cultural institutions conspire to create the impressive coordination, cooperation and division of labor of complex societies remains to be told. We suggest that a close examination of the mechanisms will reveal a series of only partially successful work-arounds of social instincts deriving from adaptation to life in much simpler, but still highly cooperative, symbolically marked groups. To the conflicts between the very small-group altruism normally favored by selection on genes and the ingroup altruism that coevolved with culture in the Pleistocene, the post-Pleistocene social institutions of complex societies add another layer of determinants of behavior that frequently conflict with all our innate social instincts.

## 7.0 References

- Alexander, R.D. (1987). *The biology of moral systems*. Aldine de Gruyter, New York.
- Axelrod, R., and Hamilton, W.D. (1981). The evolution of cooperation. *Science* **211**, 1390-6
- Barth, F. (1981). *Features of person and society in Swat: collected essays on Pathans*. Routledge and Kegan Paul, London.
- Batson, C.D. (1991). *The altruism question: toward a social psychological answer*. Lawrence Erlbaum, Hillsdale NJ.
- Bettinger, R.L. and Baumhoff, M.A.. (1982). The Numic spread: Great Basin cultures in competition. *American Antiquity*, **47**, 485-503.
- Bettinger, R.L. (1991). *Hunter-gatherers: archaeological and evolutionary theory*. Plenum, New York.
- Birdsell, J.B. (1968). Some predictions for the Pleistocene based on equilibrium systems of Recent hunter-gatherers. In *Man the Hunter* (ed. R.B. Lee and I. DeVore), pp. 229-240. Aldine, Chicago.
- Borgerhoff Mulder, M. (1988). Behavioral ecology of traditional societies. *Trends in Ecology and Evolution*, **3**, 260-4.
- Boyd, R., and Richerson, P.J. (1985). *Culture and the evolutionary process*. University of Chicago Press, Chicago.
- Boyd, R. and Richerson, P.J. (1987). The evolution of ethnic markers. *Cultural Anthropology*, **2**, 65-79.
- Boyd, R. and Richerson, P.J. (1988). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*, **132**, 337-56.
- Boyd, R. and Richerson, P.J. (1989). The evolution of indirect reciprocity. *Social Networks* **11**, 213-36.
- Boyd, R. and Richerson, P.J. (1992). Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* **13**, 171-95.
- Bryne, R. and A. Whitten (eds.). (1988). *Machiavellian intelligence: social expertise and the evolution of the intellect in monkeys, apes, and humans*. Oxford University Press, Oxford.
- Campbell, D.T. (1983) The two distinct routes beyond kin selection to ultrasociality: Implications for the Humanities and Social Sciences. In: *The Nature of Prosocial Development: Theories and Strategies* D. Bridgeman (ed.), pp. 11-39, Academic Press, New York.
- Cavalli-Sforza, L.L. and Feldman, M.W. (1981). *Cultural transmission and evolution: a quantitative approach*. Princeton University Press, Princeton.
- Cosmides, L. (1989). The logic of social exchange: has natural selection shaped human reason? Studies with the Wason selection task. *Cognition*, **31**, 187-276.
- Daly, M. and Wilson, M. 1988. *Homicide*. Aldine de Gruyter, New York.
- Darwin, C. (1874 [1902]). *The descent of man, 2nd. ed.* American Home Library, New York.
- Dunbar, R.I.M. (1992). Neocortical size as a constraint on group size in primates. *Journal of Human Evolution*. **22**, 469-93.
- Durham, W.H. (1991). *Coevolution: genes, culture, and human diversity*. Stanford University Press, Stanford.
- Eibl-Eibesfeldt, I. (1982). Warfare, man's indoctrinability, and group selection. *Zeitschrift für Tierpsychologie*, **67**, 177-198.
- Eibl-Eibesfeldt, I. (1989). *Human ethology*. Aldine de Gruyter, New York.

- Glazer, N., and Moynihan, D.P. (1975). *Ethnicity: theory and experience*. Harvard University Press, Cambridge.
- Goodall, J. (1986). *The chimpanzees of Gombe: patterns of behavior*. Cambridge Mass.: Harvard University Press, Cambridge.
- Hamilton, W.D. 1964. Genetical evolution of social behavior I, II. *Journal of theoretical Biology*, **7**, 1-52.
- Hamilton, W.D. (1975). Innate social aptitudes of man: An approach from evolutionary genetics. In *Biosocial anthropology* (ed. R.Fox), pp. 133-155. Malaby, London.
- Harcourt, A.H. (1992). Cooperation in conflicts: commonalities between humans and other animals. *Politics and the Life Sciences*, **11**, 251-9.
- Irons, W. (1979). Cultural and biological success. In *Evolutionary biology and human social behavior* (ed. N.A. Chagnon and W. Irons), pp. 257-272. Duxbury Press, North Scituate, MA.
- Knauff, B.M. (1985). *Good company and violence: sorcery and social action in a Lowland New Guinea society*. University of California Press, Berkeley.
- Knauff, B.M. (1987). Reconsidering violence in simple human societies: Homicide among the Gebusi of New Guinea. *Current Anthropology*, **28**, 457-500.
- Knauff, B.M. (1993). *South Coast New Guinea cultures: history, comparison, dialectic*. Cambridge University Press, Cambridge.
- Kummer, H., Daston, L., Gigerenzer, G., and Silk, J. (in press). The social intelligence hypothesis. In *Human by nature* (P. Weingard, S. Massen, S. Mitchell, and P. Richerson, eds.). Lawrence Erlbaum, Hillsdale, NJ.
- Maenchen-Helfen, O.J. (1973). *The world of the Huns*. University of California Press, Berkeley.
- McGrew, W.C. (1992). *Chimpanzee material culture: implications for human evolution*. Cambridge University Press, Cambridge
- Milgram, S. (1974). *Obedience to authority: an experimental view*. Harper and Row, New York.
- Nuttin, J.M., Jr., and Beckers, A. (1975). *The illusion of attitude change: towards a response contagion theory of persuasion*. Academic Press, London.
- Olson, M. (1982). *The rise and decline of nations: economic growth, stagflation, and social rigidities*. Yale University Press, New Haven.
- Otterbein, K.F. (1968). Internal war: A cross-cultural study. *American Anthropologist*, **70**, 277-89.
- Pinker, S. (1994). *The Language instinct: how the mind creates language*. William Morrow, New York.
- Rabbie, J.M. (1991). Determinants of instrumental intra-group cooperation. In *Cooperation and prosocial behavior* (ed. R.A. Hinde and J. Groebel), pp.238-262. Cambridge University Press, Cambridge.
- Rappaport, R.A. (1979). *Ecology, meaning, and religion*. North Atlantic Books, Richmond, CA.
- Rogers, E.M. (1983). *Diffusion of innovations, 3rd edition*. Macmillan, New York.
- Sepher, J. 1983. *Incest, the biosocial view*. Academic Press, New York.
- Soltis, J., R. Boyd, R., and Richerson, P.J. (1995). Can group-functional behaviors evolve by cultural group selection? An empirical test. *Current Anthropology*, **36**, 437-94.
- Tajfel, H., Flament, C., Billig, M.G., and Bundy, R.P. (1971). Social categorization and intergroup behaviour. *European Journal of Social Psychology*, **1**, 149-75.

- Trivers, R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, **46**, 35-57.
- Turner, J.C. (1984). Social identification and psychological group formation. In *The social dimension: European developments in social psychology, Vol. 2* (ed. H. Tajfel), pp. 518-538. Cambridge University Press, Cambridge.
- Silk, J.B. 1980. Adoption and kinship in Oceania. *American Anthropologist*, **82**, 79-820.
- deWaal, F.B.M. (1992) .*Chimpanzee politics*. Jonathan Cape, London.
- Westermarck, E. (1894). *The history of human marriage*. Macmillan, London.
- Wiessner, P. 1983. Style and social information in Kalahari San projectile points. *American Antiquity*, **48**, 253-76.
- Wiessner, P. (1984). Reconsidering the behavioral basis for style: A case study among the Kalahari San. *Journal of Anthropological Archaeology*, **3**, 190-234.
- Wilson, D.S. and Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences*, **17**, 585-654.
- Wilson, E.O. 1975. *Sociobiology: the new synthesis*. Harvard University Press, Cambridge.
- Wilson, E.O. and B. Hölldobler. 1988. Dense hierarchies and mass communication as the basis of organization in ant colonies. *Trends in Ecology and Evolution*, **3**, 65-7.
- Wolf, A.P. (1970). Childhood association and sexual attraction: A further test of the Westermarck hypothesis. *American Anthropologist*, **72**, 503-515.
- Yengoyan, A.A. 1968. Demographic and ecological influences on Aboriginal Australian marriage systems. In *Man the hunter* ( ed. R.B. Lee and I. DeVore), pp. 185-199. Aldine, Chicago.

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