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Human Cooperation

Perspectives from Behavioral Ecology

Eric A. Smith
Department of Anthropology, University of Washington,
Seattle, WA 98195–3100, U.S.A.

ABSTRACT

Humans, like all social species, face various collective action problems (difficulties achieving potential benefits from cooperating when coordination is required or individuals have incentives to defect). Humans solve these problems through various means: communication, monitoring, enforcement, and selective incentives. This chapter summarizes the theory and evidence on human cooperation found in the field of human behavioral ecology, categorized topically: resource sharing, cooperative production, aid-giving, and coalition-based conflict. A more speculative question is then addressed, "Why are humans so cooperative?" The suggested answers revolve around linguistic communication, technology, and coalitional behavior. In particular, language clearly increases the likelihood of solving coordination games and appears to lower the cost of monitoring and enforcement in other payoff environments. Language is also likely to enhance signaling and reputation effects. Technology and complex division of labor increase fitness interdependencies between individuals, and the potential payoffs to coalition members; these in turn provide new opportunities for development of norms and institutions to solve collective action problems. The chapter closes with some caveats about the limits to human cooperation.

INTRODUCTION

All social species face various collective action problems, i.e., various opportunities for cooperation that can yield benefits, but which can be thwarted by free riding and other forms of selfishness, as well as by coordination failures. In comparison to other vertebrates, humans appear to be remarkably good (though not perfect) at solving these collective action problems. They do so through a variety of means, including communicating about options and preferences, socially transmitting norms and other codified information, monitoring the behavior of others, imposing punishment for selfish behavior, and dispensing selective incentives for cooperative or prosocial behavior.

The means by which people manage to capture the benefits of cooperation, and the conditions under which such solutions are more or less likely to occur, are studied by analysts using several different theoretical approaches. Here I survey the approach known as human behavioral ecology, one that is complementary to but distinct from other prominent approaches to studying the evolution of human cooperation, such as evolutionary psychology and cultural inheritance theory (Smith 2000).

I begin with definition of some key terms and then outline the main features of the research strategy employed in human behavioral ecology. Next, I present summaries of behavioral ecology research in various domains of human cooperative behavior: resource sharing, cooperative production, aid-giving, and coalition-based conflict. The second major section offers rather speculative answers to the question, "Why are humans so cooperative?" The answers proffered (and interrogated) revolve around linguistic communication, technology, coalitional behavior, and kinship. I close with some caveats about the limits to human prosociality.

THE BEHAVIORAL ECOLOGY OF COLLECTIVE ACTION

Defining the Problem

In accord with the usual meaning in behavioral ecology as well as some areas of social science, I define *cooperation* as collective action for mutual benefit (Clements and Stephens 1995; Dugatkin 1997). By *collective action*, I mean whenever two or more individuals must interact or coordinate their actions to achieve some end. This end is generally to provide a *collective good*, meaning any material good or service that is then available (though not necessarily in equal amounts) for consumption by the members of some collective (e.g., a family, a village, an organization, a nation), whether or not consumption by some reduces the amount available to the remainder. Note, as defined here, cooperation does not necessarily entail (nor does it exclude) altruism, either temporary (Trivers's "reciprocal altruism") or in terms of expected lifetime fitness.

The simplest form of cooperation involves *coordination*; this applies when actors share preferences on the rank ordering of each strategy pair in the interaction and thus always mutually benefit from cooperation.[1] In behavioral ecology, coordination interactions are usually labeled "mutualism," and a distinction is often made between *by-product mutualism* (Brown 1983) where A benefits from B's action but B would perform the action and gain benefits regardless (e.g., evading predators via the "selfish herd" effect), and *synergistic mutualism*

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[1] In some fields, coordination problems are considered to lie outside the domain of cooperation, i.e., cooperation must by definition solve collective action problems where interactors have conflicts of interest (see Bowles and Gintis, this volume).

(Maynard Smith and Szathmáry 1995), where coordination yields increased per capita benefits (e.g., coordinated efforts to deter predators). A *collective action problem* (CAP) arises (a) when coordination is difficult (e.g., due to imperfect information about the actions others will take) or (b) when cooperation is individually costly but collectively beneficial (as in games of Chicken, Prisoner's Dilemma, etc.). *Free riding* consists of benefiting from a collective good without paying the costs of providing that good. A *second-order collective action problem* arises whenever the means needed to solve one CAP (e.g., monitoring, teaching, enforcement) itself poses a CAP (e.g., because it provides a collective good on which some could free ride).

Human Behavioral Ecology: Research Strategy

The adaptationist program in contemporary evolutionary biology proposes that natural selection has designed organisms to respond to environmental conditions in fitness-enhancing ways. With this as a starting point, behavioral ecologists formulate and test formal models incorporating specific optimization goals, currencies, and constraints, and use these to study evolution and adaptive design of animal behavior in ecological context. Some researchers in anthropology and cognate disciplines have adapted this approach, in conjunction with theory and method from the home discipline, as tools to analyze human behavior. Human behavioral ecology emerged in the 1970s and grew rapidly in the 1990s (Winterhalder and Smith 2000). Because it incorporates material from the much older tradition of ecological anthropology and pays some attention to the roles of intentionality and cultural evolution, it is not quite as radical a departure from standard social science as it might first appear (Smith and Winterhalder 1992).

Focusing as they do on behavior, and particularly social behavior with a strong cultural component, human behavioral ecologists must analyze a very labile and causally complex set of phenomena. They generally attempt to explain such complex patterns of behavioral variation as forms of *phenotypic adaptation* to varying social and ecological conditions. The focus is on testing predictions about the match between environmental conditions or payoffs and behavioral variation, without worrying too much about developmental or learning mechanisms that create or maintain this match. The link between such phenotypic adaptation and genetic evolution is provided by positing that the former is guided by "decision rules." These decision rules are presumed panhuman cognitive adaptations that have evolved by natural selection (or recurrent cultural evolution) and guide behavioral variation in ways sensitive to environmental context. In the language of game theory, decision rules are usually conditional strategies that take the general form "In context X, adopt one behavioral tactic; in context Y, switch to an alternative tactic," and so on. Strategies can be conditional on the actor's phenotype (e.g., "I will signal only if I am high quality") or on aspects of the social and nonsocial environment (e.g., "Ally with Joan only if she reciprocates" or "Pursue a given prey type only if it raises my mean return rate"). Behavioral variation arises as individuals match their conditional strategies to their particular socioecological settings and endowments.

Forms of Cooperation

I briefly discuss various forms of cooperation that human behavioral ecologists have analyzed, summarizing key models and representative empirical studies.

Resource Sharing

People can, of course, share a large variety of resources: land, unharvested resources, dwellings and other durable goods, labor, and so on. Research in human behavioral ecology has dealt with many of these; however, the greatest amount of research has concentrated on sharing of food in subsistence economies. Unlike most other primates, humans often harvest resources of sufficient "package size" (e.g., large game) or in sufficient bulk (e.g., an agricultural crop) that some combination of transfer to those without the resource or storage for later use is likely. A variety of behavioral ecology models are employed to analyze these phenomena (Winterhalder 1996), each making somewhat different assumptions about the socioecological circumstances specified (e.g., group size, conditionality of transfer decisions, the nature of the resource) and the evolutionary mechanism invoked (e.g., individual, kin, sexual, or trait-group selection).

Possible benefits of food sharing include risk reduction (buffering variation in individual or household food income through pooling of asynchronous and unpredictable harvests), obtaining resources without working for them (a benefit to the recipient only!), gains to trade (I produce food X more efficiently and you produce food Y more efficiently, and we mutually benefit through exchanging some of our production), and advertising the producer's quality. These hypothesized benefits correspond to distinct explanatory models from behavioral ecology: risk-reduction reciprocity, scrounging (also known as "demand sharing" or "tolerated theft"), trade, and costly signaling. Possible costs of food sharing, corresponding with the same set of explanations, include nonreciprocation (defection in a delayed-reciprocity system), exploitation (by scroungers), transaction costs (in arranging and carrying out trade), and signal costs (e.g., food income foregone or choice of a production strategy with high display value but low production efficiency).

Risk-reduction reciprocity. The Aché Indians of Paraguay have perhaps the best-documented food-sharing behavior. When studied some fifteen years ago, Aché hunters shared game evenly and without kin bias with all members of the band, regardless of foraging success. Kaplan et al. (1990) calculated that on average Aché families produced less than 1,000 calories per member on 27% of the 412 days in their sample, but after sharing only 3% days resulted in food intake below this threshold. They estimate that without food sharing, an Aché family experiencing average foraging success and variance would fail to obtain at least 50% of its caloric needs for 3 weeks running about once per 17 years. Further calculations suggest that sharing of meat increases average family nutritional status most, honey an intermediate amount, and collected foods the least; these correspond to observed rankings of sharing frequency, with meat being shared evenly in the band while collected foods are shared to a moderate degree (honey again being intermediate). While various resource qualities are correlated with sharing frequency, package size predicts much more of the resource-by-resource variance in sharing (54%) than does standard deviation in harvest success across families (23%), suggesting that Aché use package size as a robust rule of thumb for sharing decisions and/or that declining marginal value for acquirers of retaining large packages is more important that the marginal value of shares for the recipients. The net result is that "there is no discernable relationship between the amount of calories produced and the amount eaten," and the best predictor of family food consumption is number of dependents (Kaplan et al. 1990, p. 128).

Although Aché food sharing reduces consumption risk, the system is clearly not based on dyadic reciprocity. As Hawkes (1993) points out, Aché hunters do not directly control the distribution of their catch, and sharing is unconditional on foraging effort. Higher producers (i.e., better hunters) might still obtain a net nutritional gain (risk reduction that outweighs lost food income, which in case of large kills is in excess of the producer's needs); alternatively, they might be rewarded with social benefits (see below). In either case, the system of food sharing does not conform to the pattern of dyadic Tit-for-Tat conditional reciprocity envisioned in standard reciprocity theory. The suggestion that better hunters are rewarded by other band members for their production efforts and sharing raises a second-order CAP, since these rewards (e.g., greater sexual access, deference in disputes, greater solicitude for their offspring by unrelated individuals) would seem to entail private costs to those who grant them, yet provide a public good — securing the continued production of better hunters who share unconditionally with all. It is also important to note that the Aché case appears to be very unusual cross-culturally, with many other well-documented cases (e.g., Hadza, Hiwi, !Kung, Meriam, Yanomamo) lacking this extreme degree of resource pooling. Indeed, such pooling is even absent in contemporary Aché settlements (see below).

Tolerated theft. When food is acquired unpredictably, asynchronously, and in relatively large packets, at any one point in time there are likely to be "haves" and "have-nots." Given that food is likely to be characterized by diminishing marginal value to any one possessor/consumer (Figure 21.1), transfer from haves to have-nots will increase the fitness of the latter far more than it will reduce the fitness of the former. Blurton Jones (1987) suggested that under these conditions we might expect "tolerated theft" to occur, since have-nots should be willing to pay greater costs than haves in contesting resource possession. Such interactions are known as "scrounging" in the social foraging literature, and

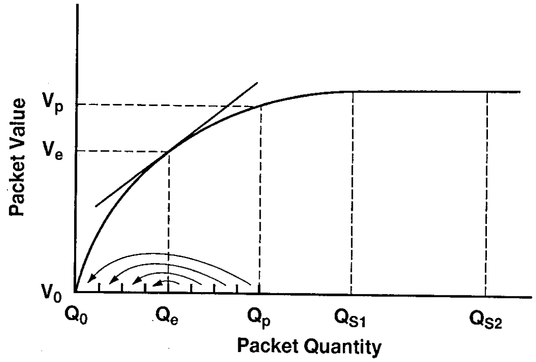

Figure 21.1 Demand sharing and declining marginal resource value in the producer-scrounger game. In the two-player case illustrated, a producer acquires a packet of size Q_p and value V_p, and relinquishes it in small portions to the scrounger (who initially has nothing, at Q_0/V_0). With equal competitive abilities (and in this simple graph, costless transactions), transfers will cease when both players attain equal marginal value and possess the equilibrium quantity Q_e. After Winterhalder (1996).

"demand sharing" in social anthropology. If contestants are of equal competitive ability, possess no other (or equal) food stores, and are characterized by equal marginal utility curves for food consumption, and if detection of harvests is immediate (or consumption sufficiently delayed), the equilibrium outcome is plausibly an equal division of the catch (Figure 21.1). If these assumptions are relaxed, the tolerated theft model will of course yield more complex predictions (Winterhalder 1996). Behavioral ecologists have modeled this process in some detail, using game theory (Giraldeau and Caraco 2000) as well as trait-group selection (Wilson 1998). Jones and others have noted that if the various relevant parameter values (e.g., competitive ability) are common knowledge, both parties may benefit by conventional solutions ("tolerating" transfers from haves to have-nots) rather than engaging in physical combat or the like — a form of mutualism nested within directly conflicting interests.

Fieldworkers disagree strenuously over the empirical relevance of tolerated theft. Whereas Hawkes (1993) suggests it is the main dynamic at work in food sharing among the Hadza (savannah hunter-gatherers of Tanzania), and Bliege Bird and Bird (1997) argue that it is better supported than alternative explanations (such as risk-reduction reciprocity) among Meriam turtle hunters of northern Australia, others find no evidence of it in the peoples they study. Thus, Kaplan et al. (1990) argue that Aché evidence contradicts tolerated theft hypotheses, in that hunters (a) actually consume less of their own production than do others, (b) return solitary kills to camp without first consuming any themselves, (c) and often call for aid upon encounter of game or honey (thus reducing their personal return rate, though often enhancing the group return rate).

Signaling. A very different explanation of sharing invokes costly signaling: by successfully harvesting and then distributing difficult-to-capture resources, individuals may reliably signal various socially important qualities, thereby benefiting themselves as well as potential allies, mates, or competitors who gain both food and useful information about the provider (Smith and Bliege Bird 2000; Gintis et al. 2001). The advantage of the costly signaling explanation is that it does not raise the collective action problems posed by reciprocity models (the threat of unilateral defection) or tolerated theft (free riding on the production efforts of others by scrounging resources). In a stable signaling system, observers will confer social benefits on signalers not as reciprocation, but because doing so is their best move: signaling indicates qualities that make it advantageous to preferentially mate with, ally with, or defer to the signaler. The weakness of signaling explanations for sharing is that the resource transfers themselves may be somewhat incidental to the signaling equilibrium; for this reason, while signaling may be a necessary component of the explanation, it is not sufficient (Gintis et al. 2001).

This apparent weakness, however, can be mitigated or eliminated under one of several conditions. First, sharing resources may serve to attract an audience, hence increasing the "broadcast efficiency" (observer per unit signal) and making the sharing a vehicle for signaling. Smith and Bliege Bird (2000) argue this is why Meriam hunters are willing to pay the entire cost of harvesting large marine turtles which they donate in toto to communal feasts hosted by unrelated clans.

Second, sharing may be somehow integral to the quality being signaled. This could happen in one of two ways: the quality being signaled might refer to the ability to generate a production surplus, or it might refer to ongoing commitment to the recipient group. Ability to generate a surplus (because of productive prowess, skilled management, or control over labor and/or resources) appears to be the key quality being signaled in many systems of communal feasting, potlatching, give-aways, and the like described in the ethnographic literature on myriad small-scale foraging, horticultural, and pastoral societies (Boone 1998). It may also play a role in the production of public goods in archaic state societies as well as contemporary electoral politics (for further discussion, see section on *Coalitions and Conflict* below). Signaling commitment to a social group by unconditionally sharing resources with its members (providing a public good) is a possibility suggested by Schelling's (1960; Nesse 2001) theory of strategic commitment, but has not yet been formally modeled or tested (Smith and Bliege Bird, submitted). The basic idea is simple enough: if I wish to convince you of my sincere ongoing commitment to a common project, I can honestly signal this commitment by contributing to the common good at levels that would not be beneficial to me were I planning on defecting over the next time period. Extended courtship (and the associated opportunity costs of time) and economic transfers such as bridewealth or dowries are straightforward examples of the phenomenon, but more subtle forms are possible (e.g., voluntarily yielding first authorship on a chapter to signal ongoing commitment to collaborative research).

Why do people share "windfall" resources more readily? A variety of lab experiments as well as anecdotes from naturalistic settings indicate that so-called "windfall resources" (those obtained by chance rather than as a result of concerted effort) are more readily shared than earned resources. For example, both Japanese and American subjects of both sexes answering hypothetical scenario questions were statistically more willing to share money (hypothetically) obtained by lottery than the same amount when it was (hypothetically) earned for participation in lab exercises (Kameda et al. 2002; see also Camerer and Thaler 1995). In effect, it appears that windfall resources are viewed as common property subject to communal sharing rules, whereas earned resources are viewed as private property that will be shared only under more stringent conditions set by the earner.

One possible explanation of this windfall-resource psychology is that it is a convention to minimize conflict costs (or more generally transaction costs) involved when resources are acquired in an unpredictable and asynchronous fashion. Kameda et al. (2003) have constructed a model for such a context, marrying the logic of Hawk–Dove games to tolerated theft. This model considers four strategies: Egoist (never share own harvest, demand a share of Other's harvest), Bourgeois (never share or demand), Communalist (always share, always demand), and Saint (always share, never demand). There is, of course, a resource of value *V*, contest costs of *C*, and group size is allowed to vary. Kameda et al. show that the Communalist strategy is evolutionarily stable under a wide range of parameter values. However, this result depends on certain assumptions, including pairwise contests followed by equal partitioning of the resource among all contestants (should the acquirer lose any contest), asymmetric conflict costs (winners pay none), and the elimination of both first- and second-order free riders via punishment.

As Kameda et al. suggest, the uncertainty involved in harvesting large game (as compared to small game or sessile resources such as plant foods) could give it the characteristics of a windfall resource, and they suggest this as the reason why a windfall psychology (or communal-sharing norm) might have evolved in *Homo*. In any case, experimental results suggest that any experiments where resources are provided by the experimenter to the subjects arbitrarily may invoke a greater propensity to share than would be the case for earned resources. This should be considered in interpreting the results of experiments utilizing the Ultimatum and Dictator games, since the stakes here are inherently unearned (windfall) resources. As Camerer and Thaler (1995, p. 216) state:

> Subjects are handed $10 in manna from experimental heaven and asked whether they would like to share some of it with a stranger who is in the room. Many do. However, if the first player is made to feel as if he earned the right to the $10, or the relationship with the other player is made less personal, then sharing shrinks.

On the other hand, windfall psychology cannot account for the much greater propensity for sharing found among hunter-gatherers than among social carnivores, nor the wide cross-cultural (and intra-cultural) variation in sharing rates for Ultimatum game players documented by Henrich et al. (2001).

How much inertia do sharing systems possess? Extant studies of food sharing in subsistence economies reveal some salient patterns: resources associated with higher production variance (e.g., big game) tend to be more widely shared, most food sharing is not structured as conditional reciprocity, demand sharing is common, and those who produce more and share more often have enhanced prestige. However, data do not unambiguously support any one of the explanations sketched above for perhaps the following reasons: (a) each food sharing system may be shaped by a different set of causal factors (risk reduction here, tolerated theft there, etc.); (b) none of the current models may be causally relevant; or (c) these systems may not be at a local optimum as a result of cultural inertia, bounded rationality, or stochastic factors. To address this last possibility, we will need detailed comparative studies, preferably diachronic ones. The best candidate to date again comes from the Aché study team.

Gurven et al. (2001) studied food sharing among Aché resident in a recently formed village of 117 people, which is comparable in size to many seminomadic or village-dwelling hunter-gatherers and horticulturalists but about twice as large as the median size of the nomadic pre-contact Aché residential groups and several times larger than the groups studied on forest treks in the 1980s.[2] Sharing patterns show a marked difference from those observed on treks: (a) any given household directs almost all its food sharing to just 2 or 3 other households (usually close relatives), and little or nothing is given to any of the other 22 households in the village; (b) there is a strong element of contingency (dyadic reciprocity) in sharing patterns — those to whom you give food are much more likely to give food to you; (c) despite the continuing egalitarian sociopolitical organization, there is no tendency for foraged foods to be shared preferentially with those who lack them. These same patterns have been documented for other settled forager-horticulturalists (Hiwi, Yanomamo, and Yora), yet they have developed very recently among the Aché, with their movement into permanent settlements. Gurven et al. argue that this dramatic shift can be attributed to a few key changes: larger group size, which increases the difficulty of detecting free riders; decreased risk (variance or unpredictability in daily food income), which reduces the payoff from pooling before consumption; and increased privacy due to home construction, which increases the ability to hide food from others and thus reduces the effectiveness of demand sharing. Although more detailed analyses are needed, this case does suggest that patterns of food sharing are very sensitive to socioecological context and can shift rapidly in response to changed conditions even in small, relatively isolated societies.

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[2] It is important to note that the Aché observed on treks in the 1980s were residing in settlements when not on trek, and group size and composition on these treks differed from that reconstructed before contact/settlement. Thus, trek data do not necessarily mimic aboriginal patterns any more closely than the data collected later in settlements.

Cooperative Production

Cooperative production, ranging from group hunting or fishing to construction of buildings or facilities (e.g., fish weirs), is a universal feature of human societies. It may offer several advantages: increased per capita resource harvest rate, reduced variation in harvest rates, reduced losses to competitors, and increased vigilance and predator detection. Cooperative production, however, can also increase resource depletion and competition; even where cooperation is beneficial, optimal group size itself may be unstable as a result of conflicts of interest between existing members and potential joiners. In any case, once groups form they provide the context for complex social dynamics, including economies of scale as well as competition and conflict over labor contributions and division of the product.

One form of cooperative production given great prominence in scenarios of hominid evolution is group hunting; behavioral ecologists have given this corresponding attention in ethnographic studies. The standard expectation has been that cooperative hunting occurs when there are economies of scale: per capita return rate R increases as a function of group size n, so that $R_1 > R_n$ for some range of n (Smith 1985). Suppose the per-capita return rate curve reaches a maximum at some intermediate group size n_{opt}, the optimal group size, and then declines gradually as n increases (Figure 21.2). Then members of a group of size n_{opt} have an interest in preventing additional individuals from joining the group, whereas potential joiners would increase their returns as long as $R_{n+1} > R_1$. This simple model thus predicts a conflict of interest between n members and a prospective joiner whenever $R_n > R_{n+1} > R_1$ (Smith 1985). The model, of course,

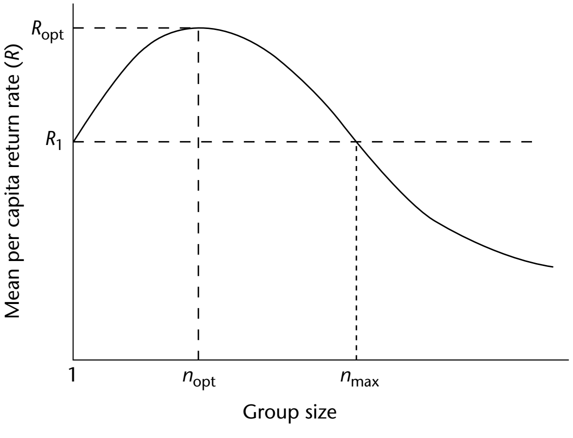

Figure 21.2 Optimal group size and member-joiner conflict. When per capita return R (a member's share of group production) reaches a maximum R_{opt} at $n_{\text{opt}} > 1$, members will benefit by restricting further entry, but potential joiners have an incentive to join as long as their share will exceed their return rate from solitary production R_1, up to the equilibrium group size of n_{max}. After Smith (1985).

Table 21.1 Group size of Inuit hunt types (data from Smith 1991, p. 316).

	Optimal group size = 1	Optimal group size > 1	Totals
Optimal group size = modal	6 hunt types	2 hunt types	8
Optimal group size < modal	2 hunt types	2 hunt types	4
Optimal group size > modal	0 hunt types	4 hunt types	4
Totals	8 hunt types	8 hunt types	16

says nothing about how such a conflict will be resolved. If members do not exclude joiners beyond n_{opt}, perhaps because exclusion presents a collective action problem, then presumably the group size will exceed the optimum (at the limit, equilibrating at n_{max}, when per capita returns are equal to R_1).

In my study of Inuit (Canadian Eskimo) hunters, I found that for hunt types where the highest per capita return rate (measured in calories per hunter hour) came from solitary hunting, the modal group size was indeed 1 in most cases (Table 21.1). For hunt types characterized by some payoff to cooperative hunting, results were quite mixed and seemed to reflect both coordination failure (where the modal observed group size was less than n_{opt}) and joiner "crowding" (where modal $n > n_{\text{opt}}$). An instructive case of the latter is beluga whale hunting, which usually occurs a day's travel from the settlement at an estuary. Hunters arrive at the hunting site in boats containing 2–3 hunters which have made the trip independently (or in coordination with perhaps one other boat) and stay one or more days. Groups smaller than 5 did not ever capture belugas, presumably because at least two boats are needed to coordinate pursuit; per capita return rate declined monotonically above $n = 6$, yet mean group size was 10.7 and groups were as large as 16. The likely explanation is twofold: lack of information makes it difficult to predict how many other hunters will be at the hunting site on any given day, and once having made the journey, hunters have no foraging options that will yield higher per capita returns even when the site is crowded (Smith 1991) — a combination of coordination failure and joiner crowding. (It is worth noting that behavioral ecologists studying cooperative hunting in nonhuman species have also had difficulty demonstrating anything that goes beyond by-product mutualism [review in Dugatkin 1997; cf. Boesch 2002].)

Alvard and Nolin (2002) report on an extensive study of cooperative hunting in the Indonesian community of Lamalera. They describe a quite complex system, involving corporate kin groups (subclans) that own traditional paddle-and-sail-powered vessels and field crews organized into specific roles (e.g., harpooner, helmsman, bailers). A set of rules specifies a very precise division of the catch, not only among the members of a successful boat crew, but also among other designated recipients (sail maker, boatwright, boat manager, and various individuals or groups with hereditary rights). Given this division of the catch (e.g., for sperm whales, 14 named shares assigned to at least 40 designated recipients) and observed hunting behavior, Alvard and Nolin calculate that whaling provides significantly greater mean returns to each crew member (ca. 0.55 kg/hr) than does the next best alternative of net fishing (0.34 kg/hr). They thus conclude that Lamalera whaling is a case of synergistic mutualism, with a payoff schedule matching the classic "stag hunt" coordination game.

Although some might view coordination games and mutualistic equilibria as not all that interesting or difficult to achieve, Alvard and Nolin (2002, p. 547) argue otherwise:

> Substantial coordination is required to subsist on cooperatively acquired resources. Behaviors must be synchronized, rules must be agreed to (even if tacitly), and assurance, trust and commitment must be generated among participants for the collective benefits of cooperative hunting to be realized.

Note, however, that in the Lamalera case the complex system of sharing rules, designated roles (e.g., boat manager), and division of labor are all necessary to ensure successful coordination of effort and hence a Pareto-efficient mutualistic payoff. These elements, in particular the sharing rules, go well beyond a simple coordination game, and in fact must have been produced by a long process of cultural evolution.

Sharing rules in hunter-gatherer societies are not often as precisely specified as in the Lamalera case. However, there are certainly norms that vary within societies (e.g., with respect to different resource types) as well as between them. The sharing rule implied in the joiner-member model outlined above is an equal division of the catch among members of the production group, with those excluded being on their own. At the opposite extreme would be a communal-sharing rule, where all producers in the band or village — whether their own production efforts were cooperative or solitary — pool and equally divide the product. The joiner-member model can be modified accordingly (Smith 1985). For simplicity, assume that the village contains N producers who can each decide whether to engage in cooperative production in a single group of size n, or to be one of m individuals engaged in solitary production ($n + m = N$). Given communal sharing, an individual share (regardless of production tactic) equals $(nR_n + mR_1)/N$. It follows that any individual will increase her production share by becoming the n^{th} member of the cooperative-production group as long as

$$nR_n + (m-1)R_1 > (n-1)R_{n-1} + mR_1 \,,$$

which simplifies to

$$nR_n - (n-1)R_{n-1} > \mathrm{R}_1.$$

This last inequality states that under communal sharing, the decision rule for production is to participate in cooperative production so long as the marginal gain in the group production rate (the left side of the inequality) exceeds the rate that can be obtained from solitary production (the right side). This stylized model illustrates how a change in sharing rules can significantly alter incentives and, in this case, dissolve the joiner-member conflict.

Ethnographic data indicate that the behavior of forest-dwelling Aché (see discussion above) closely approximates the communal-sharing rule. Consistent with the prediction just made, Aché engage in cooperative foraging (e.g., calling for aid in prey capture, pointing out resources for others to harvest, helping with prey tracking and capture) even when the act of doing so leaves the donor's return rate unchanged or lower, so long as it raises the band's overall return rate (Hill et al 1987; Hill 2002). This is particularly true for hunting and honey harvesting, but less so for gathering; again, it is well documented that Aché-gathered foods are shared much less communally than are meat and honey. Whereas Hill (2002) interprets the extensive cooperation while foraging as "altruistic" (at least in the short term), the arguments just given suggest it is simply mutualistic, *as long as the harvest is communally shared.* Of course, such communal sharing is itself a remarkable example of cooperation-in-need explanation.

While the studies summarized above provide many insights, they are couched primarily in terms of average individuals (sometimes differentiated by sex). They thus offer little insight into individual differences in constraints and opportunities that might affect decisions to participate in cooperative production. An interesting effort in this direction is a study by Sosis et al. (1998), which used bargaining theory to explain differences in individual participation in cooperative fishing production on Ifaluk atoll in Micronesia. They showed that fishing effort was lower among older men, those from higher-status clans, those with more education, and those with adult sons residing in their household, but correlated positively with need for food (as measured by household stores and numbers of dependents). These matched their predictions regarding the factors that will enhance bargaining power in interactions determining individual contribution to cooperative fishing efforts on Ifaluk. (Of course, a variety of other explanations could account for these observations.)

Aid-giving Behavior

Although aiding unrelated adult conspecifics who are seriously ill or incapacitated is reported for some dolphin species, such behavior is, in degree if not in kind, uniquely developed in humans. Darwin felt it so notable as to single it out to illustrate the unique moral evolution of our species, and paleoanthropological evidence suggests it first arose in Neanderthals and early *Homo*.

Sugiyama and Chacon (2000) studied the effect of illness and injury on foraging returns and aid-giving among two Amazonian village peoples: Yora (Peru) and Shiwiar (Ecuador). They estimate that injuries reduced foraging effort by at least 10.6% and that if a hunter of average skill is incapacitated, this reduces protein intake by 18% whereas if he were the best hunter in the group then protein intake would drop 32–37%. They note that reciprocal altruism fails to offer a convincing explanation for aid-giving (feeding of incapacitated individuals and their dependents), since the more ill one is (a) the lower the probability of survival, (b) the longer until recovery, (c) the lower the ability to punish defectors, and hence (d) the greater the temptation to defect (fail to aid the incapacitated). As Sugiyama and Chacon (2000, p. 384) put it, “in a world where only the logic of kin selection and reciprocal altruism operate, there comes a point at which abandonment of a sick or injured individual becomes the adaptive choice.” Although ethnographic anecdotes indicate that such abandonment does sometimes occur, Sugiyama and Chacon suggest that the threshold for abandonment can be increased by strategies such as costly signaling of willingness to provide public goods (e.g., sustained hunting effort and widespread sharing of the catch) and social niche differentiation to position oneself as providing irreplaceable benefits (see also Tooby and Cosmides [1996] on the “banker’s paradox”). Evidence that this occurs among Aché has been provided by Gurven et al. (2000). However, neither study provides any direct tests of hypotheses concerning mechanisms by which such a system could evolve or be stabilized. This is one area in which models incorporating partner choice (e.g., Cooper and Wallace 1998; Bshary and Noë, this volume) would seem to have much promise.

Coalitions and Conflict

Humans are arguably unique among vertebrates in the size, importance, and diversity of their coalitions. Although much coalitional behavior in small-scale societies is kin based, even this presents challenging problems for evolutionary analysis (see below). In any case, nonkin coalitions are important vehicles for within- and between-community competition in all human societies. Recent theory (Gil-White 2001; McElreath et al. 2003) and experimental data (Bornstein et al. 2002) suggest that culturally defined in-group identity, such as ethnicity, allows people to predict the presence of hard-to-observe norms and behavioral propensities, thus facilitating the solution of coordination problems. Yet what about more costly forms of cooperation? Perhaps the most striking acts of self-sacrificial cooperation in both humans and social insects occur in the context of coalition-based violent conflict, including warfare. In social insects, within-colony relatedness is usually very high, but this is not normally the case for raiding and warfare among humans.

Patton (2000) studied warfare (“intercoalitional violence”), male status, and reciprocity in an Indian community in the Ecuadorian Amazon. He found that male status is strongly correlated with warrior status (with status of both types scored by the independent rankings elicited through interviews). Unpublished data (Patton, pers. comm.) indicate that these status measures are positively correlated with reproductive success. This parallels evidence for the Yanomamo of Venezuela of a strong relationship between reproductive success and *unokai* status (marked by a public ceremony given to those who have killed an enemy on a raid): men who are *unokai* average over twice as many wives and over three times as many offspring as do other men (Chagnon 1988). Patton (2000, p. 420) argues that these social benefits of participating in coalitional violence are underpinned by a system of indirect reciprocity and reflect “an evolved strategy for the use of violence for status gain within an coalitional context." Given the doubts about how such a system of indirect reciprocity might work (Boyd and Richerson 1989; Leimar and Hammerstein 2001), we need to consider alternative hypotheses.

One such alternative is costly signaling. Proven ability in lethal fighting with enemies should be a reliable signal of the physical, emotional, and cognitive qualities that would make someone a formidable competitor. Such individuals might often be desirable allies, and competitors with lower competitive ability might find it wise to defer to them. Warriors might also be desirable mates, if their proclivity for violence is not too generalized and protection from other males has high adaptive value; in any case, they might have an easier time using alliances with, and intimidation of, other males to gain more mating opportunities. Of course, in systems (such as the Yanomamo) where some men gain wives through raiding and abduction, there can be a fairly direct link between coalitional violence and reproductive success (tempered of course by tradeoffs involving increased mortality risk).

It is important to distinguish social systems where participation in lethal conflict is voluntary and unpaid from those where military service in the rank-and-file is coerced (by conscription, threat of imprisonment, etc.) or is a source of income and upward mobility for relatively impoverished classes. The former includes the vast majority of small-scale societies, whereas all states and some chiefdoms fall in the latter category. Hierarchical societies may use various institutional means of encouraging morale and commitment (ideology, intimate face-to-face relations in modular combat units; see Richerson et al., this volume). However, given the direct incentives (threats and rewards) that motivate enlistment, the evolutionary explanation of lethal risk taking in combat among members of stratified societies is simpler (or rather, deflected to accounting for the social institutions that carry out third-party enforcement of military and political unity). In contrast, among small-scale societies, military conflict is primarily organized at the level of voluntary raiding parties led by charismatic leaders, and the adaptive payoffs include booty, captive females, and the local status enhancement noted above. (Exceptions occur in very densely populated but still small-scale societies, such as highland New Guinea.) In these systems, there is little evidence of self-sacrificial devotion to the military success of the entire society, and within-group factionalism (resulting quite often in homicide) is often common, though controlled to some extent by various institutions (e.g., adjudication by elders) as well as by threats of revenge.

Coalition-based conflict need not be violent to be important; much of political life in any society is dominated by more restrained forms of conflict. Models of political microdynamics usually assume that politicians gain power as part of a reciprocal exchange: a politician promises goods to his constituents in return for the favor of their support. Given the delayed return here ("I support you now, you return the favor by providing collective goods in the future"), defection is always a distinct possibility. Costly signaling might not eliminate the risk of defection, but it could help predict which individuals are less likely to do so: if a candidate can reliably signal a superior ability to obtain resources for redistribution, he should have a higher probability of actually doing so when elected. Here, costly signaling does not guarantee honesty of intent to deliver collective goods, but it may guarantee honest advertisement of ability to do so.

A variety of political systems, ranging from the semi-egalitarian "big man" systems of Melanesia to the stratified chiefdoms of the Northwest Coast Indians, appear to display various elements of this costly signaling dynamic of garnering political support through magnanimity (Boone 1998). In these cases, and arguably in many instances of electoral politics in modern industrialized democracies, political candidates use distributions of goods to signal honestly their ability to benefit supporters in the future. The big man, chief, or congressional candidate encourages others to donate wealth or labor in his support by displaying honest signals of his skill in accumulating resources for redistribution, thus ameliorating the most problematic aspect of delayed reciprocity, risk of default.

Whereas these arguments concern power plays within a political system, signaling may also play an important role in competition between systems. The archaeologist Fraser Neiman (1998) proposes that the florescence of monumental architecture (particularly flat-topped pyramids) among Classical Maya city-states was a form of costly signaling serving to advertise honestly the political and economic (and hence military) power of competing kingdoms. Whereas warfare was certainly common enough in these and other archaic states, Neiman argues that such provisioning of public goods served the interests of elites in competing polities by deflecting costly conflict in cases where the architectural signals indicated equally matched opponents, while simultaneously signaling the power of the elite class to the commoners within their polity.

WHY ARE HUMANS SO COOPERATIVE?

Having surveyed some relevant research in human behavioral ecology, I move now to the more speculative part of this chapter. A key question our discussion group at Dahlem sought to address is why cooperation in large groups with low relatedness is so common in humans. Various answers to this question have been proposed in the literature, including:

- a hominid population structure directly favoring the evolution of cooperation via genetic group selection (Alexander 1974; Hamilton 1975; Boehm 1997);
- genetic group selection among alternative (individually selected) equilibria (Boyd and Richerson 1990);
- cultural group selection facilitated by conformist transmission (Boyd and Richerson 1985).

As discussed by Richerson et al. (this volume), the case for the first alternative is weak. The latter two have a sounder theoretical basis (if yet untested empirically) and are ably discussed in other chapters in this volume (see Richerson et al., and Bowles and Gintis). Here I focus on alternative or complementary accounts giving central explanatory roles to language (symbolic communication) and technology.

Language and Collective Action

Symbolic communication using various linguistic media (spoken, written, signed) is a specialty of *Homo sapiens*. Most anthropologists consider it the most significant derived feature of our lineage, one that enables the transfer of large volumes of cultural information. Although communication is certainly possible without language, language allows people to communicate about events remote in time and space (including imagined futures), to express (however imperfectly) high-level cognitive abstractions and internal subjective states, and to create collectively cultural webs of meaning. Language also allows people to flatter, lie, dissemble, mislead, and obfuscate — all of which can be quite adaptive for those doing so (if not for those listening). These various aspects of linguistic communication have important implications for the forms and extent of cooperation.

Cheap Talk and Coordination

Coordination games are a relatively straightforward but underappreciated context for cooperation and the first place to look for effects of linguistic communication on cooperation. It seems almost certain that language greatly facilitates the several aspects of solving coordination problems: defining options, specifying players' preferences, and agreeing on the solution. This communication need not even be direct: I can tell Sam that Rob said he would meet him at the *Alexanderplatz* TV tower at noon, or a traffic sign can tell me which way to drive on a one-way street.

Ample evidence from lab experiments (e.g., Crawford 1998) and the real world indicates that pregame communication can significantly enhance the probability of attaining efficient solutions to coordination problems (as well as several other game forms). This suggests that "cheap talk" can be quite valuable in cases where agents share common interests:

> … solutions that include pregame negotiations are often considered trivial by economists because all humans can easily communicate in this way. From a comparative evolutionary perspective such a solution is far from trivial. The adaptive value of being able to communicate honest cooperative intent with a statement such as "I will hunt whales tomorrow with you if you hunt whales tomorrow with me" is hard to overestimate. (Alvard and Nolin 2002, p. 549)

In addition, language could be critical for defining conventions to minimize transaction costs and stabilize Pareto-superior solutions to coordination games (Alvard and Nolin 2002). When coordination games are repeated over generations, it is plausible that the locally prevalent solutions will become codified as written or orally transmitted norms that come to seem "natural" and exogenous to participants.

Signaling and Reputation Effects

Many social interactions (and the games that model these) look very different once we consider the signaling value of alternative strategies. Thus, a one-shot public goods game with a single Nash equilibrium of defection (failure of any player to provide the good) can be transformed into a signaling game where the strategy pair "signal only if high quality, provide social benefits only to signalers" is an equilibrium with a large basin of attraction (Gintis et al. 2001). As discussed above, such an analysis may explain a range of public-goods provisioning, from big-game hunting with unconditional sharing to charity galas in capitalist societies.

The role of signaling in favoring cooperation is a relatively new topic that is as yet poorly studied but is likely to be of great importance, particularly in the human case. Because of this novelty, the role of signaling effects is often overlooked. Even the venerable game of Chicken derives its name from a form of human behavior that makes little sense unless one realizes that the situation referred to (whether or not to yield to an opponent in a ritualized public contest of nerves) is nested within a larger game involving reputation effects. Such contests are not limited to 1950s American teenagers but are culturally widespread, ranging from various forms of dueling to male initiation rites to military maneuvers of state societies. (Of course, Chicken games need not entail an underlying signaling context, e.g., this is usually absent in the Hawk–Dove version analyzed in behavioral ecology.)

When signalers can derive social benefits from a number of individuals (not just a single partner), the payoffs from signaling can be greatly enhanced by some means of efficient broadcasting. Linguistic communication provides a vehicle for very low-cost (hence efficient) signaling. Instead of having to direct signals physically to observers, signalers can rely on observers to spread the word to others (e.g., the fact that Toma killed a giraffe can become known to distant parties that never tasted a morsel of that giraffe).

Of course, there is the important issue of what (if anything) ensures honesty. Much current work is aimed at understanding how low-cost linguistic communication can be linked to costly signaling theory. One proposed answer turns on social enforcement: dishonest statements can be discovered and punished (Lachmann et al. 2001). While this argument is certainly correct, it would limit the signaling value of language to situations where receivers can use other means to verify signal honesty (as well as coordination contexts where there is no incentive to be dishonest). A second proposal turns on reputation effects: if I pass unreliable information too often, you will come to discount what I say, and then I will find it difficult to influence your behavior. This is also plausible, but it can be costly for receivers while they are building up information on others' honesty, and the payoffs and dynamics here scarcely differ from nonlinguistic signaling.

With language (unlike a peacock's tail or a sparrow's status badge), you can learn something about my track record for honesty from third parties. The means by which such third-party information is transmitted ranges from gossip to testimony at public hearings to media accounts. None of these forms of linguistic communication are necessarily honest themselves, but I doubt that any have zero reliability. As with other forms of information accrual (trial-and-error learning, observation of others' behavior, etc.), individuals face a problem of statistical evaluation that they may or may not be able to solve in any given case. I would expect individuals to give greater weight to first-hand accounts of direct experience with individual X (e.g., "Sally brought me food when I was sick," "John lied to me"), and to multiple independent first-hand accounts, than to vague or second-hand accounts (e.g., "I hear Sally is a nice person," "Jane told me that John can't be trusted"). By marrying models of many-sided cultural transmission to the problem of establishing reputations for cooperation and honesty, we ought to be able to put the ideas of third-party reputation and indirect reciprocity ("standing" or "image score") on more solid footing.

Monitoring, Assortment, and Enforcement

The arguments just given focus primarily on how linguistic communication can improve outcomes in dyadic interactions, but what about multiplayer interactions that involve trust, public goods, potential for defection, and the like? I see at least three ways in which language can enhance the possibility of cooperative outcomes. First, linguistic communication might significantly lower the cost of monitoring selfish behavior in a Prisoner's Dilemma or public goods payoff environment. It is widely recognized that as group size increases beyond a very small number, the difficulty of each agent observing the behavior of all other agents makes free riding and other forms of selfish behavior much more likely to proliferate (e.g., Boyd and Richerson 1988). Language, however, allows individuals to learn about defection from other group members without having to observe it themselves directly.

Second, if language can be used to communicate information about honesty and cooperative history, then it can facilitate positive assortment of groups of cooperators. It is well known that such positive assortment can be very effective in enhancing the evolution and stability of cooperation. The problem, of course, is how to ensure reliability of the information or markers used for assortment. Language alone cannot do this (it is too easy to pretend to be a cooperator, even to oneself), but other means do exist (including the costly signaling avenue sketched above). What language can do is make it much easier to find out (with admittedly imperfect but presumably nonzero accuracy) an individual's past track record of cooperative behavior. These reputations, amplified through linguistic communication, should significantly ease the task of forming groups composed of cooperators. Again, some explicit models of this process, incorporating both linguistic communication and assortment dynamics, are sorely needed to evaluate such plausibility arguments.

Third, and perhaps most speculatively, I propose that linguistic communication can help reduce the cost of punishing defectors. The lowest-cost form of punishment is simply the third-party communication about behavior and reputation just discussed. Again, I expect this information to be of intermediate reliability and thus better than no information. Many forms of human cooperation, particularly those involving larger or variable-membership groups, rely on rules and norms that define both the rules of cooperation and modes of enforcement (including punishment). Language plays an indispensable role in formulating and transmitting these rules and norms. At the higher end of punishment cost, when punishers must directly confront defectors and impose penalties upon them, linguistic communication can at least play a role in coordinating a cooperative form of punishment. Cases where members of a hunter-gatherer band secretly plotted the abandonment or even assassination of incorrigible offenders are described in the ethnographic literature; such coordinated actions greatly reduce the per-capita cost incurred by the punishers and would be essentially impossible without linguistic communication.

Commitment

Many forms of human cooperation rely on commitments, including both secured forms such as enforceable contracts and less secured forms such as public or private promises and codes of honor (Nesse 2001). Language certainly must greatly facilitate the making of commitments, in which individuals agree in advance to a prescribed course of action, operating perhaps under a Rawlsian veil of uncertainty about what the future outcome might be. Thus, Carl and I might agree to take turns buying a lottery ticket (or going hunting), with the explicit agreement that whoever happens to succeed will share the proceeds with the other. The facilitating role of language should be particularly important for commitments to involving multiparty collective action, where nonlinguistic communication about future contingencies would be difficult if not impossible.

In addition, it seems obvious that linguistic communication also greatly expands the possibilities for advertising (and monitoring) commitments, for the reasons described above with regard to monitoring, assortment, etc. Commitments that are advertised widely (through linguistic communication) may offer advantages to the one making the commitment, and they can then be monitored by a larger audience.

Technology and Collective Action

Language may also play a critical role in making both technology and complex division of labor possible (though certainly not inevitable). By technology, I mean more than just tools; I mean a combination of tools, culturally transmitted knowledge about tool manufacture, and the use of tools in various realms, particularly in economic production.

The issue here is how technology can increase the payoffs from cooperative production. Examples from small-scale societies, even ones with "stone-age" technology, are plentiful: nets and brush or stone surrounds for game drives, fish weirs, multiperson (or multiply-deployed) watercraft, etc. Higher payoffs from cooperative production mean a greater incentive to solve collective action problems, to ensure any needed coordination, and counter free riding. Once cooperative production and other forms of (nonkin *n*-person) fitness interdependence mediated by technology and language have a foothold, they generate incentives to develop supporting social institutions and norms (Kaplan et al. submitted).

A single ethnographic example can illustrate my argument. The horse-mounted nomadic bison-hunting Indians of the North American Great Plains region are the stereotypical Indian culture of cinema and popular writing. Prior to ca. 1700, however, no such culture existed. As horses became available (after the Pueblo Revolt drove the Spanish colonists temporarily out of New Mexico), various Indian peoples migrated out onto the plains and rapidly developed a new way of life: a coadapted economy, residence pattern, set of political and religious institutions, kinship system, and so on (Oliver 1962). Within less than a century, Indians from various regions (mostly outside the plains) and with no common language or shared set of social institutions had converged on a new and distinct way of life. This lifeway, recorded in great detail by travelers and ethnographers, was remarkably adapted to the exigencies of using horses and bows and arrows (later rifles) to hunt bison, an extremely abundant (ca. 60 million) but heretofore difficult to locate and harvest nomadic herd animal.

Of particular interest here is the collective action problem posed when a tribe of several thousand people aggregated together for the summer months. The Cheyenne case is representative:

> From the time of the performance of the great ceremonies [around summer solstice] to the splitting up of the tribe at the end of the summer, no man or private group may hunt alone. During the early summer months the bison are gathered in massive herds, but distances between herds may be great. A single hunter can stampede thousands of bison and spoil the hunt for the whole tribe. To prevent this, the rules are clear, activity is rigidly policed [by a formal warrior's association], and violations are summarily and vigorously punished. (Hoebel 1978, p. 58)

A payoff matrix could hardly be clearer. Hoebel goes on to provide several detailed accounts of cases in which the rule barring selfishly "jumping the gun" was violated, and the prescribed punishment meted out (including killing the violators' horses and smashing their weapons). Again, note that these rules and institutions, brought to bear to ensure that the potential gains from collective action not be eroded by selfish behavior, had come into existence in just the few decades that elapsed from the Cheyenne abandoning horticultural villages in

Minnesota and becoming nomadic equestrian bison hunters on the Plains. They were clearly a response to a new economic opportunity afforded by the technology of mounted bison hunting and could not have existed without a symbolic cultural system based on language.

What about Kinship?

In the heady early days of sociobiology, many thought that explanations based in kin selection would unlock the mysteries of human sociality. After all, kinship — real or metaphorical — is a key organizing principle in all societies, and a linchpin for collective action in many. Inclusive fitness, however, has not proved to be the universal acid that dissolves the problems of human cooperation (nor even insect sociality). One problem is that coefficients of relatedness drop off rapidly outside a narrow orbit of close kin, whereas much of the puzzle of human sociality concerns the high amount of cooperation between members of different families (though they may often belong to the same large corporate kin group, such as a clan). Another is that kinship is often defined culturally in ways that do not line up well with the calculus of inclusive fitness. Thus, in many societies we find that unilineal kin groups (e.g., clans or lineages defined either patrilineally or matrilineally) are important foci of cooperation and within-group factionalism. Such systems seem peculiar from the standard perspective of kin selection, as they arbitrarily define half of one's genetic kin as closer cooperators than the other half.

An alternative view is that kinship is simply one of many possible conventions people use for defining in-groups in order to compete with out-groups. Yet if all kinds of arbitrary distinctions can be stable in complex games, why do people settle on kinship as the convention so often? One possible answer: given that so much of the social system in small-scale societies is based on kinship, it is a very convenient preadaptation on which to hang your coalition structure. In any case, it is a fair generalization that unilineal kin groups occur only where there are economically defendable forms of property that cannot be effectively managed or inherited in family lines (e.g., cattle herds, complex agricultural holdings, salmon streams, positions on a council of chiefs) and where formal bureaucratic structures for solving conflicts over such property rights (i.e., state systems) do not exist. In effect, unilineal kin groups are a means of forming coalitions to compete with other coalitions. If coalitions were based solely on genetic relatedness, each Ego would have a different set of preferred coalition partners (except in the limiting case of full siblings), so group boundaries would be ambiguous at best; at worst, conflicts would erupt between kin along lines defined by Hamilton's rule, and it would be difficult or impossible to hold large coalitions together (van den Berghe 1979; Alvard 2003).

Defining coalition boundaries on the basis of unilineal descent (e.g., every Ego belongs from birth to the clan of his/her mother) may solve the ambiguity problem, but in itself this does not vanquish the problems posed by cross-cutting loyalties (based on true genealogical relatedness, or other shared interests) or free-rider problems. Thus, using kinship (or ethnicity, or a variety of other conventional markers) to define group boundaries might be relatively straightforward when solving coordination problems (McElreath et al. 2003), but what is to stop a defector from free riding on the collective goods provided by kinsmen? My (highly speculative) answer is that it might be possible to extend kin-based cooperation to contexts where individual and group interests conflict if group affiliation is sufficiently costly (e.g., you won't be recognized as a member of the Turtle clan unless you undergo ritual scarification with risk of infection or donate sufficient quantities of goods to clan feasts). Under these conditions, it might not pay to fake one's affiliation, the cost only being worth paying if one is committed for the long haul. Still, this proposal is vulnerable to the question of who will enforce the cost-paying rule, as well as what to do about collective goods that are nonexcludable.

Doug Jones (2000) has developed an interesting variant on the kinship-as-group-nepotism argument. Using a combination of explicit population genetics involving multilevel selection and *n*-player game theory, he derives results that amplify kin selection and extend it to groups of various size. These results depend, however, on an exogenous solution to large-group collective action problems; in effect, they explore the implications for kin selection of having solved *n*-player collective action problems by some other means.

Limits to Cooperation

Much of the recent literature on the evolution of human cooperation extols the ascendance of prosocial norms, pro-community institutions, and innate cooperative preferences. Even allowing for the fact that some evolutionary models of the evolution of such "prosociality" are based on chronic and lethal inter-group conflict (e.g., Richerson and Boyd 2001), I suggest this picture is rather simplistic. Cooperation in human groups is far from perfect. Many social institutions and practices are grossly unfair to segments of the society (e.g., women, the poor, subjugated castes, and ethnic groups). Free riding, socioeconomic exploitation, and other inequalities with major fitness consequences are well-known features of state societies. Ethnographic evidence indicates that at least some of these are also common in small-scale (nonstate) societies, though at arguably lower levels. For one thing, monitoring of and sanctions against antisocial behavior are universal, which in turn suggests selfish behavior is also ubiquitous. Within-group homicide rates can be very high in stateless societies (or in areas where the state is weak), and these often concern disputes over adultery, theft, "honor," or alleged witchcraft (rather than enforcement of prosocial norms).

According to some accounts, conformist cultural transmission and/or enforcement of prosocial norms act to reduce fitness differences drastically within groups, thus facilitating group selection (Boehm 1997; Wilson 1998; Bowles and Gintis, this volume). However, quantitative evidence from various societies with egalitarian or semi-egalitarian sociopolitical structure (Aché, Achuar, Hadza, Hiwi, !Kung, Meriam, Yanomamo) reveals substantial differences in at least male reproductive success (Smith et al. 2003). This suggests to me that resource sharing and other egalitarian elements in small-scale societies may have less impact on fitness differentials than some have proposed. Indeed, various explanations of resource sharing — risk reduction, costly signaling, tolerated scrounging, as well as bargaining dynamics in dominant-subordinate relations — indicate that giving away some portion of one's resources may offer higher marginal fitness returns than hoarding them. Interpreting resource (and power) sharing as prosocial "leveling mechanisms" (Bowles and Gintis, this volume) may mask the prime evolutionary forces that shape such behavior, as well as their fitness consequences.

In sum, conflict, exploitation, free riding, and reproductive skew appear to be much more pervasive in small-scale societies than is commonly realized and large-scale collective action much less common. (In state societies, exploitation and inequality is generally more institutionalized, but conflict management and large-scale cooperation are facilitated by segmentation into smaller groups where trust and enforcement is more likely, as well as by third-party enforcement with selective incentives for enforcers.) Humans may be much more cooperative than baboons or chimpanzees, but the evidence suggests to me that the gap is not so vast as portrayed in some accounts.

CONCLUSION

As Richerson and Boyd (2001, p. 212) note, the unique features of human sociality "cast into question explanations that should apply widely to many other species…. If a cheap, honest, cooperative signaling system evolves in a straightforward way, then we should expect many species to use it, and cooperation on the human pattern should be relatively common." The point is well taken, and the challenge is to provide evolutionary explanations for human cooperation that are powerful enough to explain the empirical evidence without being so broad as to predict identical outcomes in other species.

Currently there are several plausible accounts for the evolution of human cooperation. I have nominated symbolic communication and the fitness interdependencies arising from technologically mediated complex division of labor as species-specific elements that shift human behavioral ecology toward more intensive and larger-scale cooperation. These elements arose in the context of yet poorly understood evolutionary transitions creating our species (and its immediate predecessors), a transition in which natural selection favored the ability to produce surplus resources and expand the scale of social interaction, which in turn required solving collective action problems that other species have not managed to overcome. Several participants at this Dahlem Workshop propose a crucial role for group selection (cultural and/or genetic) in generating the intensified cooperation of our species; however, given the lack of development of alternatives, I would argue this remains an open question. Our theoretical possibilities are rich, but meaningful evaluation of these will require expanded model-building and empirical testing.

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