

ALTRUISTIC COOPERATION DURING FORAGING BY THE ACHE, AND THE EVOLVED HUMAN PREDISPOSITION TO COOPERATE

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This paper presents quantitative data on altruistic cooperation during food acquisition by Ache foragers. Cooperative activities are defined as those that entail a cost of time and energy to the donor but primarily lead to an increase in the foraging success of the recipient. Data show that Ache men and women spend about 10% of all foraging time engaged in altruistic cooperation on average, and that on some days they may spend more than 50% of their foraging time in such activities. The most time-consuming cooperative activity for both sexes is helping during the pursuit of game animals, a pattern that is probably linked to the widespread sharing of game by Ache foragers. Cooperative food acquisition and subsequent food redistribution in hunter-gatherer societies are critical behaviors that probably helped shape universal, evolved, cooperative tendencies that are well illustrated in modern experimental economics.

KEY WORDS: Ache; Altruism; Cooperation; Food acquisition; Foraging; Hunter-gatherers; Sexual division of labor

Little is known about cooperative food acquisition in foraging societies, despite the fact that modern economies are heavily based on cooperative production by groups of individuals who alone could not achieve the product obtained cooperatively, or could not do so at the same level of efficiency. Indeed, only a few studies present quantitative data on

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cooperation during food production for any modern foraging society (e.g., Alvard 2001; Bailey 1991; Ichikawa 1983; Smith 1991) or small-scale tribal agricultural society (see Sosis 2000; Sosis et al. 1998). This lack of data on foraging cooperation is surprising in light of the fact that food sharing is often thought to be partly due to cooperative acquisition and has therefore been studied in detail (see Gurven 2000; Hawkes 1993; Hill and Kaplan 1993; Kaplan and Hill 1985).

The lack of information about cooperative acquisition in foraging societies is unfortunate because a long evolutionary history of cooperative production in foraging societies is probably responsible for the universal human tendency to cooperate, as observed in recent cross-cultural economic experiments (Henrich et al. 2001). Data on foraging peoples will be critical for assessing whether certain behavioral mechanisms that produce cooperative tendencies could have evolved in the history of our species. Modern economic experiments suggest that people often cooperate in anonymous, one-shot games where noncooperation would lead to highest payoff for any individual player, but cooperation leads to highest mean payoff for all players (Caporael et al. 1989; Dawes and Thaler 1988). Such results are referred to in economics as "anomalies" (Thaler 1992) because they are not consistent with the rational, self-interested decision making that is the basis of most modern economic theory. Most important, cooperative economic strategies are commonly adopted in a variety of economic games (experiments) in which players obtain higher payoffs when all cooperate than when all don't cooperate, but highest payoffs can be obtained by those who defect on cooperative partners (i.e., classic Prisoner's Dilemma payoff structure). In such experiments cooperation is high whenever interactants know each other, when strangers are allowed to become slightly familiar prior to interacting (Bohnet and Frey 1999), when responses of fellow interactants are known (Gächter and Fehr 1999), when interactants belong to the same artificially created group (Dawes et al. 1988), when they are allowed to communicate with fellow interactants before or during the experiment (Dawes and Thaler 1988; Orbell et al. 1988), or when they can punish noncooperative interactants (Fehr and Gächter 2000a, 2000b). In almost all cases listed above, strong incentives come from group approval or disapproval, and Boyd and Richerson (1992) have shown that punishment alone is sufficient to obtain evolutionary stability for almost any costly social norm.

Human cooperation is so ubiquitous that people appear to have a sense of "fairness" that contradicts predictions from rational self-interest models in economics and is unparalleled in nonhuman organisms. This is illustrated by several outcomes in recent economic experiments, such as (1) the willingness to divide resources with anonymous partners who cannot retaliate if no division takes place ("dictator" game; Forsythe et al. 1994),

or who are known to be unlikely to retaliate (“ultimatum” game without rejections; Henrich et al. 2001); (2) the willingness of a potential recipient to reject resources from divisions in which the divider keeps a large fraction of the total stake, if rejection punishes the divider (“ultimatum” game with rejections of amounts greater than zero; Camerer and Thaler 1995; Fehr and Gächter 2000a); and (3) the willingness to pay a cost to punish individuals who do not cooperate in the production of public goods, even if no further interaction with those individuals is possible (“public goods” games with punishment in the final round; Fehr and Gächter 2000b). Particularly notable is the willingness to punish those who behave unfairly, even when the punishment comes at an extremely high cost to the punisher. For example, Cameron (1999) shows that some players will reject offers in the ultimatum game that they consider unfair even when their rejection costs them the equivalent of a month’s salary! These general results are found in modern societies and in a variety of traditional societies with limited exposure to the modern capitalistic market system (Henrich et al. 2001), including the Ache foragers described in this paper (Hill and Gurven 2001).

In addition, recent studies on the development of cooperative behavior in children suggest that children go from uncooperative to a hypercooperative phase prior to reaching an adult phase of contingent cooperative behavior (Camerer 2001). Thus, the available data on human cooperation suggest the possibility that humans have an evolved predisposition to (1) seek cooperative solutions which will benefit all interactants relative to the alternative payoffs from noncooperation; (2) share the resources cooperatively acquired by groups of individuals who are defined as belonging to the same economic “group,” or resources individually acquired in which the identity of the initial acquirer of the resource is partially or wholly determined by luck; and (3) punish noncooperative exploitation of cooperators, or unwillingness to divide gains that are understood to belong to all, even when punishment is costly. These traits characterizing interactions between adult non-kin seem particularly well developed in humans relative to any other mammal and are probably ultimately based in evolved psychological mechanisms unique to our species (Cosmides and Tooby 1992).

The assessment of cooperative behavior requires a clear-cut definition of what constitutes cooperation. Many actions are described as “cooperative” in the animal behavior literature, ranging from simple synchrony of activity to incurring a cost in order to benefit another individual (see Boesch and Boesch 1989; Rothstein and Pierotti 1988, 1989). In this study, all activities which required some time or effort and *appeared mainly designed to raise the foraging return rate of another adult or unrelated child* were coded as “cooperative foraging.” This definition explicitly excludes

opportunistic synchrony of activities by individuals when that synchrony might increase the gain rate of all individuals who behave appropriately. While such "mutualistic" behavior is common in some animals that have been described as "cooperating" (see Connor 1986), I do not think such behavior requires any special explanation beyond immediate, short-term, self-interested strategizing. But, explaining the evolutionary stability of temporarily costly acts of cooperation between non-kin in which both parties face serious temptation to defect for short-term gain requires more complex theoretical models (e.g., Mesterton-Gibbons and Dugatkin 1992).

In order to understand many special characteristics of our species that possibly led to its replacement of other hominids and unique biological dominance in the modern world, we must examine how humans acquired the adaptive tendency to rapidly seek out cooperative solutions that can bring advantage, and to quickly detect and punish those who fail to cooperate in such situations. In this paper I present preliminary data on cooperation during foraging by Ache hunter-gatherers of Paraguay. The data suggest that foraging cooperation is widespread and intense, accounting for a substantial fraction of total foraging time and including a high number of potentially costly acts that are performed on a daily basis. The levels of Ache cooperation during food acquisition are much higher than those ever observed for any other primate. Cooperation also includes some actions that are not very costly to the donor but are highly beneficial to the recipient. Most important, the cooperative patterns observed during food acquisition are almost certainly related to the well-studied Ache food-sharing patterns (Gurven, Hill, and Kaplan 2002; Gurven Allen-Arave et al. 2000, 2001; Kaplan and Hill 1985). Reward for foraging cooperation takes place in the form of food redistribution. Finally, cooperation during food acquisition represents only a fraction of the total cooperative activities in Ache society. Indeed, cooperative food acquisition, food sharing, and cooperation in other realms, such as child rearing, mobility, camp construction, and defense, are all part of an integrated system of reciprocal altruism among the Ache in which goods and services are "traded" across all fitness-enhancing activities, leading to a socioeconomic system which would probably outcompete any alternative not based on extensive cooperation. If immigrants to such a system were "forced" to cooperate through punishment and sanctions, foraging societies with such cooperative arrangements would probably rapidly replace those without them (Boyd 2001; Soltis et al. 1995).

ACHE FORAGING AND SHARING

The Ache are a foraging people belonging to the Tupi-Guarani linguistic family and living in the forested areas of eastern Paraguay (Hill 1994; Hill

and Hurtado 2000). They had only sporadic and hostile interactions with neighboring horticultural Guarani Indians until the late twentieth century. At that time, when they made first peaceful outside contact, the Northern Ache population block was expanding rapidly into areas depopulated by Brazilian slave raiders in the seventeenth and eighteenth centuries (Hill and Hurtado 1996). From earliest Jesuit accounts in the 1600s until contact in the 1970s the Ache were nomadic foragers living in small bands and depending entirely on wild forest resources for subsistence (however, they did occasionally raid the manioc fields of their neighbors). They share only one Tupi-Guarani cognate for a domestic crop (corn), thus suggesting a long period of isolation from agricultural societies. After contact in the 1970s the Ache were intensively studied by ecological anthropologists, who have published more than 50 articles on topics such as foraging decisions, time allocation, sexual division of labor, food sharing, mating patterns, demography, and life history patterns (see Hill and Hurtado 1996 for a review). Since this paper reports cooperative food acquisition on forest treks when study subjects were subsisting entirely on wild resources, I provide information only on the Ache forest economy rather than the reservation settlement economy that now dominates Ache life.

The Northern Ache consisted of about 560 people who roamed an area of about 15,000 km² of broadleaf forest just prior to peaceful outside contact in the 1970s. Prior to contact these people resided in about 10–15 different bands, whose membership was highly fluid. All adults knew and occasionally interacted with all other adults in the population. All people outside this population block were considered enemies to be shot on sight. Typically residential bands were made up of between 15 and 60 individuals (McMillan 2000) who moved camp every day at times, but also frequently remained in a single spot for a few days or even a week before moving a few kilometers to a new campsite. Bands often split up for a day or two to forage for specific resources in known locations, then reuniting to share the proceeds of their forays. Residential bands fissioned and fused with other bands regularly.

The Ache forest economy is based on hunting wild game and extracting palm starch and growing shoots from palms that are purposely cut to provide a substrate for insect larva. During the early wet season honey extraction is also important, and gathering activities in the middle wet season are focused for a few weeks at a time on collecting the fruit of a half dozen or so primary species. During the peak dry season, palm fruit and wild volunteer oranges (originally brought to Paraguay by the Jesuits) are collected.

The general daily pattern of the Ache is for men and women to leave a campsite together. After about 20 minutes, the men usually separate from the women and continue walking together. Slowly some men branch off from the main group and go to the left or right, fanning out but continuing in a direction previously agreed upon. After about 45 minutes most

men are searching alone or in pairs (often with teen boys as well), but most of them keep close enough to the others to maintain occasional auditory contact. When prey are encountered men will often call for help from nearby hunters, particularly if the prey is a group of monkeys, coatis, or peccaries. Some men usually stay with the women and children's group to open up a trail; climb fruit trees; cut palm logs for hearts, starch, and larva; and extract honey. Because the women and children usually follow the men's group they may catch up to game pursuits, and hunters visit the women's group throughout the day to deposit prey and then return to hunting. Women with no small children will sometimes stay with their husbands throughout the day, helping in search and pursuit of game. And finally, on some days whole families branch off from the main foraging party and head for a previously located resource (usually a honey tree or larva patch) that they will exploit and then share with the remaining band members when they reunite later in the day.

Energetically the most important component of the Ache diet is wild game, which made up about 78% of the daily caloric intake in the forest during the 1980s and 1990s (Kaplan et al. 2000). During this sample period the most important game animals by biomass were nine-banded armadillos (35%), cebus monkeys (13%), paca (16%), white-lipped peccaries (8%), coatis (6%), and tapir (10%). Typically men acquired about 4 kg of meat (live weight) per day. However, the probability of a single hunter not killing any game on a particular day was about 40% (Hill and Hawkes 1983); thus families were dependent on each other for food on a daily basis. On only a few days was no game killed by any hunters in a residential band during a sample of more than 300 days of forest foraging, and never did a stretch of two days pass without game being acquired by several hunters.

Cooperation during hunting is common and critical to successful hunting of some species. Men usually coordinate their prey search patterns to stay within earshot of each other, and they often search together in pairs or small groups during part of the day. They call other men to help them when they find pacas, monkeys, white-lipped peccaries, coatis, and sometimes armadillos (depending on how complicated the pursuit may be). These animals make up about 80% of the biomass acquired by hunters. Preliminary analyses suggest that forming pursuit groups for four of these species increases the total food available to the band (Hill and Hawkes 1983; McMillan 2000). Because of the cultural convention of band-wide sharing of game items, calling other men over to form cooperative pursuits for some animals also increases the expected food intake for the family of the hunters who originally found these prey. Casual observation suggests that the magnitude of payoffs to calling or responding to calls about game encounters varies considerably by species. Importantly, call-

ing for help during pursuit of some species appears to lower the expected return rate of the caller but increase the return rate of the responders. And, for some species, responding to a call for help probably lowers the expected foraging return rate of the respondent but increases the return rate of the finder. In other words, both calling and responding may at times constitute short-term altruism. Men also call other men to help them when they find honey. These cooperation patterns are probably critical for understanding subsequent food sharing and will be discussed in more detail below.

Palm starch is extracted by women from trees which are felled by men. Although palms are quite common in the Paraguayan forest, patches of "good" palms that may have high starch content are rare and many campsites are not located near exploitable palm patches. Thus, on many days, no palm starch is obtained. When a good patch is found, about 15–20 trees must be felled in order to discover one with inner fiber high in starch content. The growing shoot of each of these trees is usually extracted by the man who cut it, while women accompanying the man (usually his wife and a few other women) test each tree for starch. Starch content cannot be determined without felling a prospective tree and cutting open a section about three-fourths of the way up the trunk, pounding the trunk fiber with the back of an ax to soften it, and then tasting the pounded fiber. When a tree high in starch is discovered the trunk is split open and one or two women extract all the fiber along about a 5–7 m section of the trunk. The extracted fiber is then taken back to camp, usually in loads of about 20 kg per woman, and then mixed with water and squeezed by hand to extract the starch. This starchy water is boiled and mixed with meat or insect larva. When cool, the mixture resembles a mildly sweet, but greasy, pudding (*bre'e*), which is the main carbohydrate staple of the Ache diet. Although small amounts of palm fiber eaten at the extraction site are usually shared mainly with family members, large batches of palm starch brought back to camp and processed into *bre'e* are usually shared with all band members.

Honey is extracted using smoke to disorient the bees. In precontact times, men often climbed trees to extract honey high in the branches using scaffolding or vines to tie themselves in place. Now, more commonly men call for help and take turns chopping down the tree, chopping open an access window, and pulling out the honey comb. Women and children assist by cleaning the honeycomb of dead bees and wax parts that contain no edible honey or larva. They also pack the comb and carry it. The whole process usually takes 1–3 hours for two or more men and nets up to about 20 liters of honey in the peak season.

Fruits are gathered opportunistically by women and children during the wet season, and occasionally by men while hunting. Usually a teenage boy

or older man who is not hunting will accompany the women and children's group and climb the tree to shake down fruits that can then be collected from the ground. Men and small children generally collect only enough for consumption on the spot, whereas women and older children will often collect for longer periods and stash some fruit in a container which is later divided mainly among family members. When the collectors consist of only a subset of the band's women and children they are more likely to collect large quantities which are brought back to be shared with the band members who remained behind.

Larva are generally extracted from trees that have been cut specifically so adult palm beetles can lay eggs in the rotting trunks. Men return to a stand of palms previously cut for palm starch when they think that larva will be plentiful (usually after a few months). Sometimes men and women work together to extract larva by splitting open the palm trunks and searching through the rotting fiber. In such cases the man does the chopping and the woman searches for the grubs. If women and children extract larva without the help of a man, a strong woman will do the chopping while other women and children search for the grubs. Whenever larva are found in large quantities the bulk is tied up in leaves and taken back to the main camp to be shared with members who were not present at the extraction site.

The food-sharing patterns of forest-living Ache have been described in previous publications (Gurven et al. 2002; Kaplan 1983; Kaplan and Hill 1985; Kaplan et al. 1984). Ache hunters often abandon their game at the edge of camp when they return from the hunt. Animals are cooked by the hunter's wife or other women (especially pregnant women, who often name their unborn child for an animal they cooked). When the meat is cooked an older male (not the hunter) usually divides it up into pieces, or piles of pieces, and hands them out, often with the help of another male who calls out the names of each family that should receive a share. Other band members are quick to remind the distributors which family has yet to receive a share (they never mention themselves, only others that they know have not eaten yet). All meat is pooled and shared equally among adult band members; however, the hunter of the game usually does not eat from his own kill. Wives and children of hunters receive no greater portion of meat than any other individual in the band. Single men and women are given smaller portions, and families are given larger portions depending on how many children they have. Children between the ages of about 7–20 with no resident parents may be slighted and receive no share or a very small share, especially if their biological father is dead. Teenage boys who don't hunt are not guaranteed a share, but those who hunt seriously (i.e., all day long) receive an adult share. Recent data analyses (Gurven et al. 2002) confirm that there are no long-term relationships between how much meat is received from any other family and how much is given to

that family (i.e., no evidence of giving to a specific family that is contingent on receiving). Nevertheless, receipt of a share may be contingent on participating in the sharing network, since it is my impression that those who refuse to share game would probably be expelled from the band.

Palm starch pudding is also shared in the same pattern as meat except that the husband of the woman who cooked the pudding often distributes the portions. All other plant and insect resources are shared differently, with no taboo against eating one's own production, a tendency for the producer to keep more for his/her family than is given to other band members, a strong trend for the fraction shared to increase with package size, and a statistically significant relationship between the amount shared to specific nuclear families and the amount received from them (Gurven et al. 2002). Both men and women systematically collect more of these non-meat resources than they intend for their nuclear family to consume. There are no sex differences in sharing patterns once resource type and package size are controlled.

COOPERATION DURING ACHE FORAGING

Methods

In order to provide an estimate of time spent in cooperative acquisition by Ache men and women I carefully coded data from field notes of focal person follows on forest treks in 1981–1982 and tapes of recorded data from focal follows on forest treks in 1997–1998. The sample is 50 man-day focal follows (21,315 minutes) and 20 woman-day focal follows (6,173 minutes). After cooperative events were identified, time spent in each “cooperative bout” was summed for each sample day. Short events (such as telling somebody something) were coded as one minute in duration. Cooperation is defined as expending time and energy in an activity that seems mainly designed to increase the food return rate of another individual. In some cases “cooperative activities” might also increase the foraging gain rate of the “cooperator” (while simultaneously increasing another individual's gain rate as well). These events are treated separately from those that can only increase the foraging gain rate of the “recipient” of cooperation. Total time in cooperative activities was divided by total foraging time (time spent out of a residential camp on that day) on each focal person-day in order to calculate percentages of total foraging time dedicated to cooperative activities.

Cooperative activities during foraging time included the following adult interactions: cuts a trail for others to follow; makes a bridge for others to cross a river; carries another's child; climbs a tree to flush a monkey for another hunter; allows another to shoot at prey when ego has first (best) shot; allows another to dig out an armadillo or extract honey or larva

when ego encountered it; yells whereabouts of escaping prey; calls the location of a resource for another individual to exploit while ego continues searching; calls another to come to a pursuit of a peccary, paca, monkey, or coati; waits for others to join a pursuit, thus lowering own return rate; tracks peccaries when ego has no arrows (for other men to kill); carries game shot by another hunter; climbs fruit trees to knock down fruit for others to collect; cuts down palms (for others to take heart or fiber); opens a "window" in a tree to test for palm starch (for others to come take); carries the palm fiber others have collected; cuts down fruit trees for others to collect the fruit; brings a bow, arrow, ax, or other tool to another in a pursuit; spends time instructing another on how to acquire a resource; lends bow or ax to another when it could be used by ego; helps to look for another's arrows; prepares or repairs another man's bow and arrows in the middle of a pursuit; goes back on trail to warn others of wasp nest; walks toward other hunters to warn of fresh jaguar tracks or poisonous snakes; removes dangerous obstacles from the trail before others arrive. Helping juvenile offspring was quite common for both sexes but is not coded as cooperation in this analyses because it is best considered parental investment and is probably common in most social mammals that allow their offspring to feed with them.

Note that the estimate of cooperative time presented here is a minimum estimate since these data were not originally collected with a focus on recording all cooperative activity. Short cooperative activities were especially unlikely to be recorded in field notes. For example, examination of video tapes from hunting episodes during the sample period reveals that very short cooperative activities are frequently embedded in longer hunting segments that we have not coded as cooperative time. While pursuing monkeys, hunters often call to others to "stay put," "don't make noise," "don't shoot," "shake a branch," "pound a vine," etc. Other multi-hunter pursuits contain numerous similar requests. The recipient of such a command almost always complies at least momentarily, resulting in a cost to his own chances of making the kill. These events were extremely common but of very short duration (usually only 10 seconds or so) and are not included in the analyses.

Results

Ache men spent an average of 41 minutes per day (s.e. = 7) in food-acquisition activities scored as cooperative, and women spent 33 minutes per day (s.e. = 14) cooperating in foraging. This represents about 10% of total foraging time in the men's sample and 11% of total foraging time in the women's sample. The frequency distribution of focal person-days (Figure 1) shows that while zero time in cooperation is the most common cat-

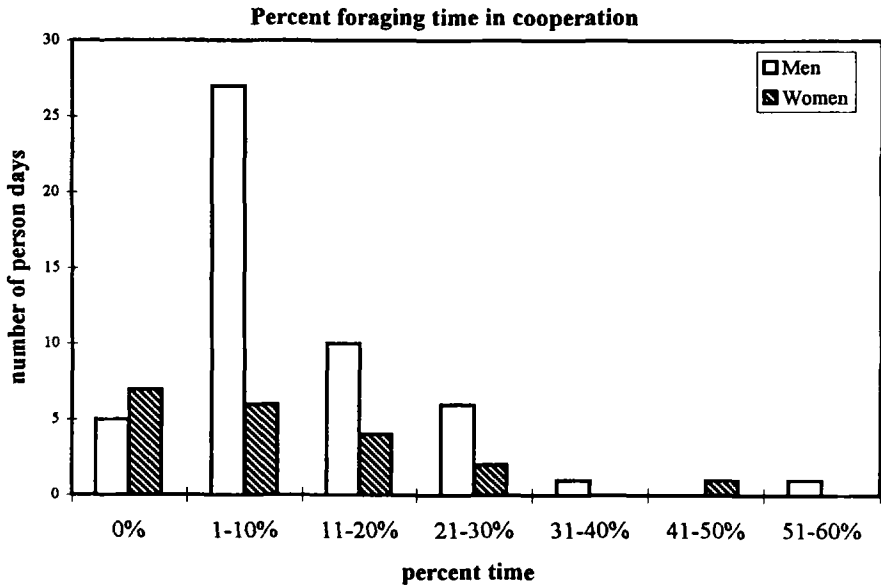


Figure 1. Frequency distribution of percent foraging time spent in cooperative activities on each day for Ache men ($n = 50$ person-days) and Ache women ($n = 20$ person-days).

egory for women, and less than 10% of foraging time in cooperative food acquisition is the most common for men, both sexes show some sample days with close to 50% of total foraging time being spent helping other individuals to acquire resources.

Analyses of whether cooperative behaviors are purely altruistic (in the short term) or whether they might also sometimes increase the foraging gain rate of the cooperator show that in the vast majority of events coded (for men, 70% of total cooperation time; for women, 96%) the behavior helped another individual but not the cooperator. In a smaller fraction of the cases, both the cooperator and a recipient might be helped by the cooperator's actions (for men, 13% of cooperation time; for women, 4%). These events included cases such as climbing a tree to shake down fruit for others (but also consuming some fruit in the tree) and building a bridge for others to cross (but using it as well). Finally, in some cases (17% of men's cooperation time) we are still not sure whether the action taken primarily increases the foraging gain rate of another individual or whether it is also designed to increase the gain rate of the cooperator. These cases included events such as helping in an armadillo pursuit when called by the finder who will probably make the kill (but the helper may occasionally be the

one who makes the kill) and calling for multiple helpers in a paca pursuit when preliminary data suggest that pursuing the animal alone or with only one helper would probably lead to a higher individual return rate from the pursuit. These events are potentially cooperative foraging, but further analyses of collected foraging data is required.

Another interesting dimension of cooperation by men and women is an analysis of who is helped in cooperative bouts. In particular, our impression is that a good deal of cooperation in foraging takes place between spouses. This impression is partially upheld by analyses of our sample, but there are large differences between the sexes. For example, 55% of women's cooperation time was spent in activities designed to help *only* their husbands increase their foraging gain rate. But, men helped *only* their wives in 6% of all cooperation time. Since the trips analyzed had a mean of 6.3 adult women and 9.3 adult men per band, if cooperation was distributed randomly among adults, both adult men and women should spend 6.6% of their time helping spouses. Men and women also spent some time in cooperative activities that could help both a spouse and other adults (21% of men's cooperation time, 4% of women's). These events included activities such as men shaking down fruit for the cooperator's wife and other women to collect and women spotting monkeys in a hunt in which their husbands and other men are involved. Cooperative behaviors that are designed to help adults other than one's spouse were more typical of men's cooperation time than women's (for men, 73% of all cooperation time; for women, 42%).

Unlike spousal cooperation, helping close adult kin was not an important component of the cooperative time recorded in our Ache sample. Only 1% of men's cooperative time and 2% of women's cooperative time was dedicated to actions that helped only adult siblings. None of the time in our sample for either sex was spent in cooperation designed to help only adult offspring or a parent.

In order to estimate the relative importance of different types of cooperative activities we lumped all events into the following nine categories for men: helps in hunt, cuts/clears/makes trail, helps extract honey, cuts palms for others, makes/repairs/lends tool, carries/tends another's offspring, shakes down fruit, provides information (mainly about resource location), and takes action to reduce danger to others. Events were divided into those of extremely short duration and those that take longer than one minute. The percentage of men's total cooperative time spent in activities of each category is shown in Figure 2. Helping another during a hunt (pursuit of prey) was the most common cooperative activity of either short or long duration. Helping extract honey or palm products, or clearing the trail, were also common activities of long duration, and providing information about resource location was a common cooperative event of short

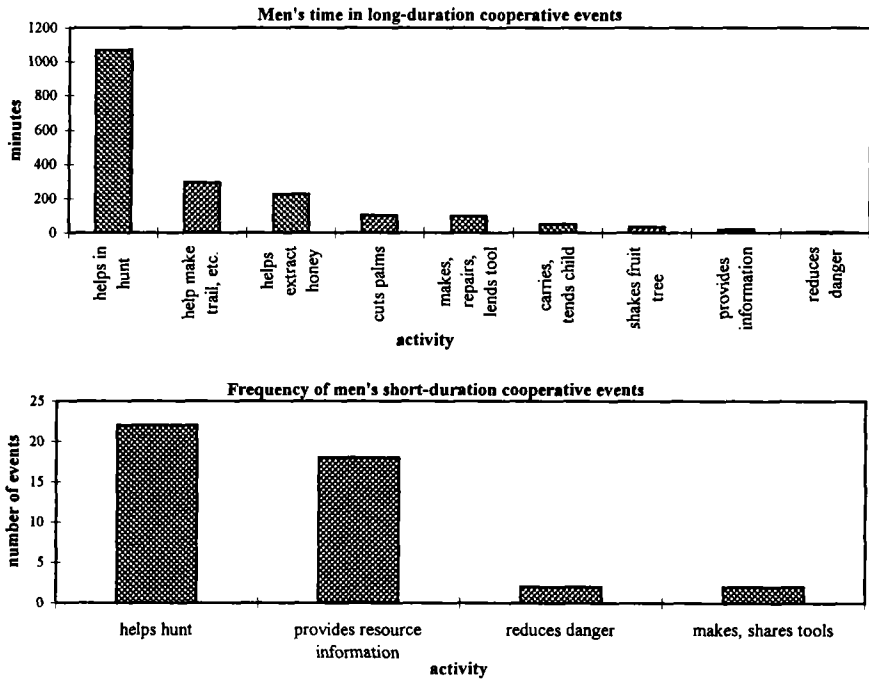


Figure 2. The relative importance of different categories of cooperative behavior for Ache men. Total minutes from the entire sample spent in longer activities is shown in the upper graph; number of events from cooperative activities that took less than one minute is shown in the lower graph.

duration. Other categories are considerably less time-consuming but may have important fitness consequences nevertheless. For example, providing information about snake or jaguar encounters, moving thorny vines out of the trail, breaking off sharp stumps in the trail, and killing wasp nests ahead of others or marking a trail around them all have important health consequences even though the actions may take less than a minute of the cooperators' time.

Women's cooperative activities were lumped into these eight categories: helps in hunt, does childcare for another, loans tools, helps extract honey, cuts palms for another, provides information about resource location, teaches another how to extract a resource, and takes action to reduce danger to others. Again events were divided into those of very short duration and those that took more than one minute. The most common of the latter was helping in a hunt (pursuit) whereas the most common short cooperative event was providing information to another about resource location

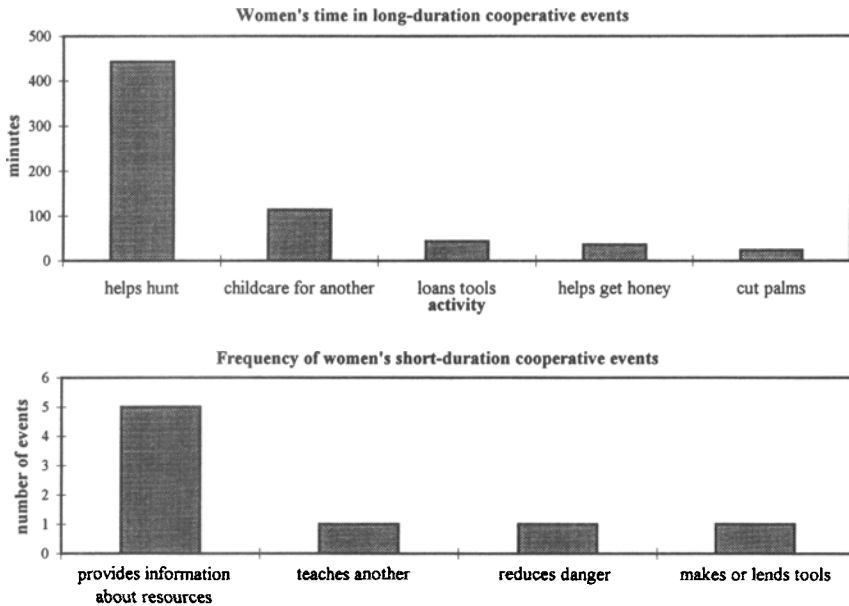


Figure 3. The relative importance of different categories of cooperative behavior for Ache women. Total minutes from the entire sample spent in longer activities is shown in the upper graph; number of events from cooperative activities that took less than one minute is shown in the lower graph.

(Figure 3). The next most common event of at least one minute in duration was caring for another's child during foraging bouts.

Although most of these cooperative events are designed to help another individual acquire food more efficiently, there is considerably more cooperation with some food types than others. The Ache diet consists of six major resource types: game, honey, palm starch, palm hearts, fruits, and larva. The data show that about 72% of men's total cooperative time and 81% of women's total cooperative time is dedicated to helping another obtain game (Figure 4). The next most important cooperatively acquired resource is honey, followed by large batches of palm fiber. Fruits, palm hearts, and larva extraction represented very little of the total time spent in foraging cooperation.

IMPLICATIONS FOR COOPERATIVE FOOD SHARING

It seems intuitive that high degrees of cooperation during food acquisition should lead to high levels of food sharing. Why should an individual help

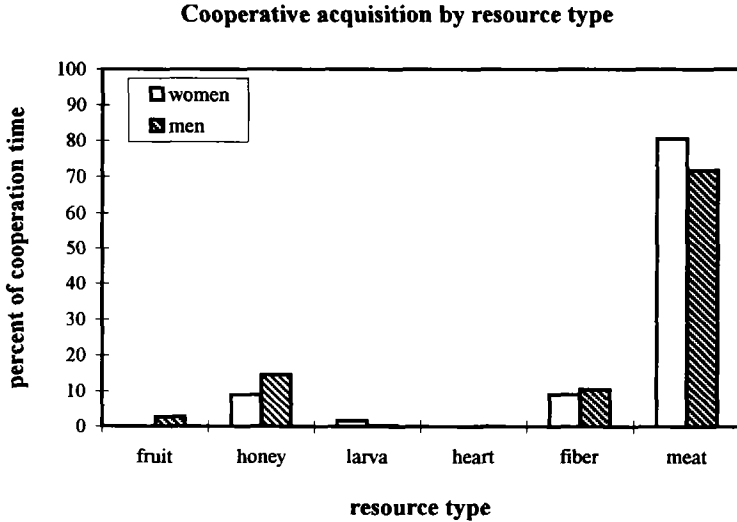


Figure 4. Percent of total cooperation time for men and women dedicated to helping acquire each of the main food types in the Ache diet.

another to acquire a resource if he or she is unlikely to consume any of that resource? Likewise, if an individual receives help in acquiring a resource and hopes to receive help again in the future, an obvious enticement to the cooperators is a share of the resource obtained through cooperation. Thus, if cooperation produces more total food per forager than solitary foraging, an informal bargain linking cooperating to food sharing will result in higher food consumption by both parties than if no bargain is struck and foragers fail in pursuits for lack of cooperative help. Although it is possible that sharing takes place only through tolerated theft, but potential recipients still cooperate in order to ensure successful production that they can later parasitize, such a system would be open to free-riding. Highest payoffs would be obtained by foragers who never paid the costs of cooperating but always obtained a share of foraged resources.

I suspect that this problem is solved among humans by making sharing contingent on labor contributions. Empirical data from experimental economics clearly show this trend to be common. First, cooperation is commonly observed in economic experiments in which the average reward to all players is higher when all cooperate (Fehr and Gächter 2000b). Second, Dawes and Thaler (1988) found that individuals were quite willing to invest in the production of a public good, *even when there was no guarantee that the public good would be obtained*, as long as they were guaranteed a “fair” share of the good if it was obtained. This seems analogous to an

agreement for all men to hunt cooperatively, even when failure in the pursuit of game is possible, as long as each cooperator can expect an equal share in the event of a kill. Likewise, in economic experiments labeled "trust" games, one individual can pass money to a second player with the understanding that that contribution will be increased by some factor. The second player can then pass any amount back to the first player. First players commonly "trust" second players to redistribute gains from their contribution and thus contribute substantially (Berg et al. 1995; Camerer 2001; Fehr et al. 1993). Importantly, the redistribution by the second player is generally related to the level of contribution (i.e., cooperation) by the first player. Thus, those who pay a cost to increase the resources obtained by another (i.e., cooperate) receive more back in subsequent voluntary redistribution than those who pay no cost. And, the share received is an increasing function of the cost paid by the cooperator.

The human tendency to reward those who have helped increase one's own reward is also seen in some primate studies. For example, cebus monkeys in separate cages who receive help from a cooperator to acquire food often share some of their reward with the cooperator by passing it through the wire mesh (Brosnan and de Waal 2002). Likewise, Tai chimpanzees who make a kill during cooperative hunting are reported to share more meat with other males that performed important helping functions during the pursuit (Boesch and Boesch 2000:179).

Clearly, however, forest-dwelling Ache share food resources to a remarkable degree not matched in other quantitative sharing studies. Indeed, game is shared almost equally to all families in a residential band regardless of who makes the kill (Gurven et al. 2002; Kaplan et al. 1984). Other non-meat resources are shared slightly less extensively, but acquirers still keep less than 50% of the resources they acquire on average. In an earlier publication we concluded that cooperative acquisition did not explain high levels of Ache food sharing because cooperatively hunted game species were not shared any more than game species that are killed by single hunters (Kaplan et al. 1985). However, that conclusion may have been erroneous because it was based on a very restricted model of how cooperation might be related to sharing. It assumed that only specific resources that were acquired cooperatively would be widely shared.

Instead, I now suggest that the Ache may share all foods partly because of pervasive cooperation during *all* phases of foraging (from clearing the trail for others to frequently pointing out resources for others to acquire). That cooperation, along with the important nutritional effects of reducing the amount of variance in daily intake, probably entices all to accept a bargain in which any individual who has participated in attempting to acquire resources is entitled to a share of those resources. Although consistently successful producers end up subsidizing less-successful producers

in this arrangement, they may still be better off nutritionally than in situations with no food sharing at all. Within this generalized cooperative production and sharing pattern there are also specific reciprocal exchanges of other foods that are contingent on shares received by others (Gurven et al. 2002) and a variety of other goods and services that flow between food-sharing partners. Finally, some resource flows may also be partially due to the benefits of costly signaling or even tolerated theft.

Our data support an informal model of Ache food sharing that relates cooperative acquisition to levels of redistribution. The three resource types that accounted for most of the cooperative foraging time are also the three that are most widely shared among Ache foraging bands (Figure 4; Kaplan et al. 1985). And, game resources, which account for about three-fourths of all cooperation time, are uniquely shared equally among all band families regardless of who actually kills the animal. The Ache seem to have adopted a rule of thumb for hunted resources: "cooperate frequently and share fully." Perhaps this rule of thumb is favored because it avoids the costs of accounting (who owes whom how much when cooperation is frequent and complex) and the cost of errors that might eliminate cooperation if attempts are made to assess cooperative versus noncooperative behavior by other individuals. I suspect that the only way to defect on this cooperative arrangement in Ache society is not to forage at all.

The Ache predispositions to cooperative acquisition and sharing seem to emerge in economic experiments played with that population for monetary prizes. Ache adults on average offer almost half of the initial stake in the ultimatum game, and a significant number of individuals offer even more than half the initial stake (much like hunters who give away most of what they kill). This is true despite the fact that no offers in that game were ever rejected; thus stingy redistributors are not punished directly by unhappy recipients. In the public goods game most players invested nearly half their initial stake in order to increase overall winnings to the group, even when that was costly to them as individuals (these results are from Hill and Gurven 2001). This appears similar to the cooperative rules of thumb that govern Ache food acquisition patterns.

Thus, I think that much of the documented Ache food sharing is induced by broad levels of cooperation in all food acquisition as well as non-foraging activities. Individuals who attempt to acquire food that will be shared with others appear to have "rights" to shares of food in the Ache moral system. This intuitive system of reciprocity includes even anthropologists, and probably explains why the anthropologists who were doing fieldwork among the Ache often attempted to acquire food while they were collecting data, and why those who didn't know how to forage often attempted to help in other ways (collecting firewood, getting water, carrying things, etc.). Finally this arrangement is so natural to humans that it

probably explains why all anthropologists who worked with the Ache felt compelled to provide gifts to band members who had fed them during forest treks when the researchers were mainly taking notes and not assisting in the hunt.

We cannot directly test the proposition that men in Ache society are expected to hunt in order to receive a share of game because we have never observed men refuse to hunt unless they had a serious illness. Data from other societies suggest that the social bargain of "attempt to bring in food in order to have rights to widely shared foods" is common. Among the Gunwiguu of Arnhem Land (Altman 1987) and the Siriono of Bolivia (Holmberg 1969) shares were withheld from lax individuals until they increased their effort to expected levels. Among the Ache, teenage boys are sometimes threatened that if they do not attempt to bring in game they will not receive a share of game killed by other men. This is particularly true now that many Ache adolescents have attended school and are not competent hunters owing to lack of experience in the forest. In one case we observed a young man in his early twenties attempt to hunt three days in a row without ever bringing in anything. Indeed he did not encounter anything but small birds and one small rodent on two of these days, but he continued to carry a bow and leave camp by himself early each morning. At the end of each day he was encouraged by men and women alike, who voiced strong approval of his attempts to contribute game despite his growing depression at his lack of hunting skills. He was given a full adult share of food at the end of each foraging day. Over a period of about two years we observed another adolescent boy progress from zero production to moderate success at killing two species of animals. During that time he was a frequent hunting companion with whom other men always shared their game.

CONCLUSION

The Ache study presented here is a first attempt to quantify the types and levels of cooperation that take place in a foraging society during food acquisition activities. We suspect that some foraging societies are characterized by lower levels and others by higher levels of cooperation than the Ache, depending on local ecology and technology. For example, Hiwi foragers that we have observed virtually never hunt alone. All men hunt in pairs or larger groups, and a good deal of foraging is also carried out by spouses working together. Most Hiwi hunting is done from a canoe, with one individual paddling while another shoots at prey with a bow and arrow. Even Hiwi terrestrial foraging often includes canoe travel to a resource patch, and during the canoe travel both individuals must cooperate to arrive quickly. But, unlike the Ache forest bands where all men hunt

every day, most Hiwi foraging days include only a few pairs of men or spouses hunting together, with most adults remaining in camp engaged in other activities. Sharing of meat resources among the Hiwi is also much more restricted than among the Ache, with only a few individuals receiving shares from any game item that is acquired (Gurven, Hill et al. 2000). Importantly, cooperating partners almost always receive a share in Hiwi meat distributions, even when only a small amount of game is acquired and no other individuals in the camp receive a share.

It is risky to speculate about the amount of cooperation typical in human foraging societies during the hundred thousand years of our species' existence. But it seems likely that cooperation during hunting might have been even more important prior to the invention of projectile weapons. Hunters in many modern foraging societies search for game by themselves and shoot prey items from a distance with poisoned, metal-tipped arrows or firearms. They subsequently seek help from other hunters only to track wounded game or carry it back to camp. But with less lethal weapons, cooperative hunting techniques were probably much more common in earlier human foragers. Indeed, it is very difficult to imagine how some of the large game species present in hominid archaeological assemblages could ever have been killed without cooperation.

In any case, forager cooperation is not limited to hunting, nor even food acquisition. Ache foragers commonly engage in extra-foraging cooperation and probably include the exchange of all goods and services in their informal assessments of the value of cooperative social partners in daily life. Non-foraging cooperation in Ache forest camps includes services such as clearing a camp spot for others; bringing water for others; collecting firewood for others; lighting or tending another's fire; cooking and food processing for others; building a hut that others share; making, fixing, and lending every imaginable tool; grooming others; keeping insect pests away from others; tending others' infant and juvenile offspring; feeding another's offspring; teaching another's offspring; caring for others when they are ill; collecting medicinal plants for others; listening to others' problems and giving advice; providing company for others who must stay behind in camp or go out to forage alone; and even entertaining others (singing, joking, telling stories) when requested.

High levels of short-term altruistic cooperation seem to be much more common among humans than among any other primates. Although other animals may occasionally synchronize their activities such that individuals gain higher payoffs through synchrony, such activity should not be lumped in the same category as the types of cooperation described here. Most human cooperation is based on the performance of altruistic acts followed by the expectation of later reciprocation. Solitary animals such as mice can learn to synchronize their activities with other animals if there is

a payoff (Schuster 2002). These behaviors do not require any special explanation equivalent to those required to explain human cooperative foraging. Indeed, these animals can learn to synchronize their behavior with members of any species, and even with lights, sounds, and other cues in a Skinner box, if there is a payoff.

In contrast, Ache cooperative foraging consists of short-term sacrifice to help individuals who are genetically unrelated (or distantly related). Sometimes episodes of helping are not "paid back" for long periods of time (days, weeks, months) and are repaid in ways that are often not explicitly directly linked to prior events of cooperation. But most foragers keep informal track of who owes them favors and to whom they owe favors in return. Humans seem to be predisposed to look for cooperative solutions that can bring long-term advantage to cooperators, and they are skilled at assessing the potential benefits of cooperation. Economic experiments suggest that humans are also predisposed to assume that most other humans (even strangers) are cooperators until proven otherwise, and that they are willing to pay a price to punish those who are not (Fehr et al. 2002). They seem particularly skilled at assessing the likely payoffs from cheating on cooperative arrangements and at paying attention to signs that other individuals are attempting to defect on a cooperative convention (Cosmides and Tooby 1992).

All these behaviors are a part of universally recognized norms of fairness in human societies, and this complex of traits appears fully developed in foraging societies. Data on cooperation in foraging societies are therefore critical to understanding how such tendencies evolved. This paper is a first step in documenting this link. Clearly more theoretical work is required to explain why cooperative tendencies in the face of temptation to defect on cooperation are common in experimental economics and how an Ache-like system of foraging cooperation, food sharing, and "fairness" can emerge from the less cooperative social system that must have characterized our primate ancestors.

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