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Current Anthropology, Vol. 26, No. 2 (Apr., 1985), 223-246.

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Food Sharing among Ache Foragers: Tests of Explanatory Hypotheses¹

by Hillard Kaplan and Kim Hill

THE SHARING OF FOOD is a phenomenon of theoretical interest to both anthropologists and students of nonhuman animal behavior. Anthropologists have long noted the pervasiveness of food sharing and other forms of resource exchange in human social groups, particularly in pre-state societies (see, for example, Lévi-Strauss 1969, Malinowski 1922, Mauss 1967, Sahlins 1972, Service 1966). While few quantitative data exist on the extent of food sharing in different societies, ethnographic reports suggest that it is both widespread and cross-culturally variable (see, for example, Binford 1978, Damas 1975, Gould 1981, Hart and Pilling 1960, Landes 1961, Lee 1979, Marshall 1961, Woodburn 1982). In spite of this variation, the pervasiveness of food sharing in human social groups has led several anthropologists to speculate upon its importance in shaping the unique character of human sociality (Kitahara-Frisch 1982; Lee 1979:490; Lancaster 1978; Washburn and Lancaster 1968; Zihlman 1983). In fact, Isaac (1978) has proposed that the establishment of home bases for the purpose of food sharing and food processing approximately two million years ago was a critical causal step in the evolution of language, intelligence, and the sexual division of labor.

Parallel to this interest in food sharing among humans has been a growing concern for understanding its occurrence in

¹ This research was supported by L. S. B. Leakey Foundation grants to Hillard Kaplan and Kim Hill and by NSF and NIH grants to Kristen Hawkes. We would like to thank A. M. Hurtado and Kristen Hawkes for their enormous help in collecting the data. Father Wayne Robbins at Mission Chupa Pou and Graciela Ocariz in Asunción helped immensely to make our field period enjoyable and productive. We would also like to thank Eric Charnov, Ray Hames, and Kristen Hawkes for their comments and criticisms on early drafts of the manuscript.

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The present paper was submitted in final form 28 vi 84.

nonhumans. The last two decades have witnessed an explosion in the data available on food sharing and related forms of assistance giving in animals, particularly among birds and mammals (for reviews, see Brown 1978, Emlen 1978, Ligon 1983, Reidman 1982). This empirical research has been stimulated, in part, by recent theoretical attempts to examine the conditions under which food sharing and related phenomena could evolve. Specifically, the reevaluation of the likelihood of group- or species-level adaptation has led to a series of developments in specifying the conditions under which assistance giving, in general, could evolve with selection operating at the level of individual organisms (e.g., Axelrod 1981; Axelrod and Hamilton 1981; Hamilton 1963, 1964; Trivers 1971; Williams 1966; West-Eberhard 1975). Nevertheless, many questions remain unanswered, particularly regarding the factors which pattern *variation* in the extent to which food is shared within and across species. Moreover, there still exists a gulf between traditional anthropological approaches to the understanding of food sharing among human groups and those of theoretical biologists who attempt to account for similar phenomena among organisms in general. This paper is intended to help bridge that gap and to make some contribution both to the data base on food sharing and to our understanding of the principles which pattern its occurrence.

The paper has two interrelated goals. The first is to apply the logic of evolutionary ecology to a problem of human social relations and to evaluate the extent to which theory and data derived from research with nonhuman animals generate productive hypotheses for understanding variation in food sharing among human social groups. The second is to test alternative hypotheses regarding the evolution of food sharing with data collected among a group of human foragers. Given the reported pervasiveness and variability of food sharing among hunting and gathering groups and the observation that some resources are shared more than others (Binford 1978, Bose 1964, Damas 1975, Gould 1981, Lee 1979, Marshall 1961), the study of human foragers should provide an excellent context for isolating some of the factors which determine the occurrence of food sharing among organisms in general. Ache hunter-gatherers of eastern Paraguay have been shown both to share their food extensively and to exhibit significant variation in the extent to which different foods are shared (Kaplan et al. 1984). This variation will be analyzed to test the predictions of alternative hypotheses proposed to explain the evolution of food sharing. The general problem to be investigated is: What factors determine the presence and extent of food sharing among adult conspecifics? (Provisioning of children by their parents will not be addressed directly.) The hypotheses to be tested will be derived from both the evolutionary ecological and the anthropological literature.

FOOD SHARING AMONG NONHUMANS

In the following overview of current approaches to the problem of food sharing among nonhuman animals, our aim is to isolate the predictions of various models concerning the factors which govern the sharing of food so that those predictions can be tested against the data collected with Ache foragers.

Four principal sets of conditions have been proposed by evolutionary biologists to account for the evaluation of food sharing: benefits to kin, tolerated theft, reciprocity, and cooperative acquisition.

Kin selection. Hamilton (1963, 1964) has specified the conditions under which selection will favor the giving of assistance to genetically related individuals. He argues that selection favors assistance when the fitness benefit to the receiver divided by the cost to the giver is greater than the reciprocal of their genetic relatedness ($B/C > 1/r$). This formalization implies that if food sharing is to be favored by kin selection, the fitness value of food to individuals who are genetically related must be asymmetrical (i.e., the value of the shared food must be lower to the giver than it is to the receiver). It also implies that the degree of asymmetry necessary for food sharing to be selected will be inversely proportional to the degree of genetic relatedness between givers and receivers.

Given these conditions, it is not surprising that the overwhelming majority of food sharing occurs between parents and offspring. Since immature organisms should be least able to acquire food for themselves and would therefore benefit most from receiving food and since offspring are closely related to their parents ($r = .5$ among sexually reproducing organisms in noninbred populations), the transfer of food from parents to offspring is most likely to meet the conditions specified by Hamilton. In fact, parents share food with offspring among all sexually reproducing organisms, at the very least in the form of energy stored in the ovum.

Yet, while parent-offspring food sharing is a constant, the length and intensity of its occurrence vary markedly across animal taxa. Among birds, for example, in some species in which young are precocial no food is provided by parents other than that stored in the egg, whereas in others (large raptors, for example) young may be fed by parents for two years after birth. Among mammals, food transfer from parents to offspring is typically high as a result of internal gestation and lactation, but the extent to which parents provision young varies with such factors as body size, life span, litter size, and degree of altriciality of young (see Eisenberg 1982 for a detailed discussion).

The literature examining the ecological conditions which affect the extent of parental investment in offspring, too extensive to review here, indicates that this variation is due to ecologically variant trade-off functions between increased reproductive investment in a single offspring or brood of offspring and the apportionment of that investment in the production of additional offspring. These trade-offs, in turn, are affected by the opportunity costs incurred by investment, on the one hand, and by the benefits to offspring of investment, on the other. Provisioning should occur up to the point that an additional unit of provisioning would yield a lower fitness payoff than an equivalent unit of investment in the production of additional offspring. Thus, other things being equal, in species in which young are altricial and benefit more from provisioning, we should find smaller clutch sizes and higher levels of provisioning than in species in which young are precocial. Empirical data support this prediction (for reviews, see Eisenberg 1982, Lack 1968, Wittenberger and Tilson 1980), although it is still not clear whether altriciality is generally a cause or an effect of parental investment.

Similarly, different resources should be differentially shared with offspring according to the costs and benefits associated

with providing them. In general, parents should share with offspring resources that young cannot acquire easily but that are acquired without difficulty by adults. Data on chimpanzees support this hypothesis; maternal provisioning of offspring occurs most frequently with resources that are very difficult for juveniles to acquire or process. While a great deal of work remains to be done regarding the factors which affect parental food sharing, hypotheses based upon ecologically variant costs and benefits appear to be the most productive avenue of approach.

Perhaps the second most common form of kin-selected food sharing, with the possible exception of adult-adult food sharing among eusocial insects, occurs between young and their older siblings or their parents' siblings. Again, this is probably because young animals have the most to gain from food sharing. This pattern is particularly prevalent among territorial nesting birds, although there is some controversy regarding whether it is kin selection or some other selective advantage which is responsible for its evolution and maintenance in stable populations. Most proponents of the kin-selection hypothesis (Brown 1974, 1978; Emlen 1978) suggest that this form of food sharing occurs when restriction of reproductive opportunities for the givers reduces the opportunity cost associated with food sharing. This would typically occur when establishing a territory is a prerequisite for mating or successful reproduction and territories are in limited supply. The best available option for an individual who is unable to establish a territory might be to feed the young of close kin.

These predictions are largely met by the data. Most "helpers at the nest" (adults and subadults who provision and otherwise care for the offspring of other birds) are closely related to the young they feed and care for (for reviews, see Brown 1978; Emlen 1978, 1981; Orians, Orians, and Orians 1977). Moreover, most cases in which juveniles are fed by individuals other than their parents conform to the pattern of limited territory availability. Helping at the nest has, however, been reported for colonial-nesting birds, which do not establish separate territories. For example, helping at the nest has been reported for white-fronted bee-eaters when the helpers' own nests have been destroyed by some natural disaster or when their broods fail to survive (Emlen 1981). Here, again, because the breeding season is not long enough to permit rearing a second brood once the first one has failed, it seems that food sharing and other forms of caring among related individuals occur when opportunity costs are low, thus increasing the ratio between indirect fitness benefits and fitness costs.

A similar phenomenon has been reported for social carnivores, particularly canids, hyenas, and lions. Among wolves, jackals, and African hunting dogs, pack members, generally closely related individuals, collectively regurgitate food for the young who remain at den sites (Frame et al. 1979; Kleiman and Eisenberg 1973; Kuhme 1965; Mech 1970; Moehlman 1980). Of particular interest here is that there is typically only one breeding pair per pack. Dominant males prevent their brothers and sons from mating, and breeding females attempt to do the same with other females. That subordinate individuals feed the offspring of the breeding pair when breeding adults prevent them from mating may also involve reduced opportunity costs. If hunting or scavenging large game requires several individuals either to kill the prey or to defend it from other predators, subordinate individuals may not have the option of leaving the pack and breeding elsewhere. If this is the case, feeding the young of the breeding pair to whom they are closely related will be the best available option for maximizing their inclusive fitness.

Hyenas have also been reported to share food with related young (Kruuk 1972, Mills 1982, Owens and Owens 1979). Some males among brown hyenas have been reported to remain permanently with their sisters and feed their sisters' offspring by carrying portions of kills back to them (Mills 1982).

Presumably, many of these males never leave their natal pack and thus never reproduce. In contrast, other males leave their natal packs and roam solitarily or in pairs until they secure a mate, who will most probably be living with brothers, sisters, and developing young. This seems to provide an excellent test case for the kin-selection opportunity-cost hypothesis. If the risks associated with nomadic status (increased risk of predation and of starving) are high, then variation in such factors as individual fighting and hunting ability, population density, and the number of dependent young for which the sister or mother is currently caring should affect the cost/benefit ratio of provisioning related young versus seeking breeding opportunities elsewhere. These factors might predict variation in the options observed.²

Given the perspective outlined above, kin-selected food sharing should be least common among adults. Other things being equal, the disparity between adults in resource acquisition ability should be lower than that between adults and young, particularly when size, strength, and learned skills are important in acquiring resources. Thus the indirect benefits associated with giving food to related adults should be lower than those associated with giving food to related young. This seems to be largely true. However, food sharing among related adults is common among social carnivores, particularly among wolves, hunting dogs, hyenas, and lions (Frame et al. 1979, Kleiman and Eisenberg 1967, Kruuk 1972, Kuhme 1965, Mech 1970, Owens and Owens 1979, Schaller 1972, Van Lawick and Van Lawick 1970). The size and unpredictability of the food resources exploited by social carnivores (who tend to consume prey larger than themselves [Clutton-Brock and Harvey 1978]) may be critical here. For a lion who has just killed a zebra, the value of one of its legs should be significantly lower than for her sibling who has not made a kill.

In sum, the following expectations about kin-selected food sharing are suggested by the data on nonhuman animals: the degree of asymmetry in resource value necessary for selection to favor kin-based food sharing is inversely proportional to the degree of genetic relatedness between givers and receivers. Young organisms are most likely to be the recipients of food from kin (particularly from their parents) because they tend to benefit most from shared food. Ecological variation in such factors as the character of the resources exploited and the type of mating system should have profound effects upon the costs and benefits of sharing food with kin.

Tolerated theft. Tolerated theft has been proposed to explain the outcomes of contests over divisible resources, such as food, when there is an asymmetry in the value of the resources to contestants (see Maynard Smith and Parker 1976, Maynard Smith and Price 1973, and, especially, Blurton Jones n.d.). Other things (such as fighting ability) being equal, the contestant to whom the resource is more valuable should win the contest. This is because there is a trade-off between the costs associated with fighting over the resource and the benefits of obtaining or keeping it. If costs are equal for the contestants, then benefits should determine who is willing to fight longest

and hardest for the resource and should therefore determine the outcome of the contest.

This model has been primarily applied to the case in which resource value follows some sort of diminishing-returns curve (fig. 1), that is, in which a point is reached where an additional unit of that resource is less valuable than earlier units. Food clearly seems to possess this quality: the fiftieth kilo should, in general, be less valuable than the second kilo (in the absence of storage or trade). Given that the fitness value of food diminishes as the amount increases beyond some point, asymmetry in the value of food between potential contestants should occur when food resources come in large packages which are sporadic in their occurrence. When some individuals acquire large amounts while others acquire none or little, the tolerated-theft hypothesis predicts that possessors will permit nonpossessors to "steal" from them because the cost of defense to the possessor is greater than the value of retaining the "stolen" portion.

Empirical data are consistent with the prediction that package size and nonsynchrony of acquisition predict extensive food sharing among adults. As mentioned above, the most extensive adult-adult food sharing among higher animals occurs with the social carnivores, whose feeding pattern is characterized by both large package size (relative to the body size of the consumer) and nonsynchrony of acquisition among individuals. In addition, consistent with the tolerated-theft model, dominance status is reported to determine, at least to some extent, the distribution of food at kills among wolves, lions, and African hunting dogs. Among both wolves and hunting dogs, while all adult pack members appear to receive a share of the kill, the dominant male is reported to occupy the "preferred" position at the carcass (Mech 1970, Frame et al. 1979). Male lions often supplant females at a kill site and eat until they are apparently satisfied (Schaller 1972).

Large package size and nonsynchrony of acquisition also seem to predict variation in adult-adult food sharing among baboons and chimpanzees. While neither chimpanzee nor baboon adults share food regularly, the relatively rare mammalian kills are shared extensively (Hamilton and Busse 1981, Harding and Strum 1976, Strum 1981, Teleki 1973, Wrangham 1975). Large fruits which occur in small quantities are also shared more extensively than other resources among adult pygmy chimpanzees (Kano 1980); most plant foods are shared mainly between mother and offspring (McGrew 1975, Silk 1978).

Reciprocity. Trivers (1971) has proposed a set of conditions under which seemingly "altruistic" behaviors could evolve in the absence of genetic relatedness. According to Trivers, reciprocal altruism is predicated on the condition that (1) individ-



FIG. 1. Food value in relation to amount available for consumption.

² Lions are also reported to live in matrilineal kin groups (Bertram 1975, 1976; Schaller 1972). Females have been observed to nurse the young of other females in the pride and to carry them to kill sites to feed (Bertram 1975, 1976; Schaller 1972). Whether kin selection or some form of reciprocity is involved in the evolution of this behavior remains to be determined (the same question may be asked of the indiscriminate nursing of sisters' offspring observed in elephants [Douglas-Hamilton and Douglas-Hamilton 1975]). One interesting difference between lions and most social canids is that whereas only one pair generally breeds and clutch size is relatively large among social canids and hyenas, most females in a lion pride breed and clutch size is small. Why do we not observe smaller clutches and multiple breeding pairs among social canids or vice versa for lions? Answers to this question should provide interesting insights into the relationship between reproductive competition, kin selection, and food sharing.

uals bear some cost which benefits other individuals; (2) the individuals who bear the cost receive some benefit from the individuals they benefit; and (3) for both individuals, the benefits are higher than the costs. At least two classes of reciprocity, presenting different problems in terms of its selection, may be distinguished.

1. In "tit-for-tat" reciprocity, perhaps the more widely recognized form, a unit of value is transferred from one individual to another in exchange for an equivalent unit in the same fitness currency at a later point in time. In order for this form of reciprocity to be favored by selection, two conditions must be met: (1) for each individual, the value of the unit received is greater than the value of the unit given; (2) individuals who do not reciprocate achieve a lower net fitness than those who do.

Condition 1 will obtain when the value of a unit of some resource varies over time. In the case of food, this is likely to occur as a function of abundance. As in the case of tolerated theft, if the value of a unit of food diminishes as amount increases, temporal variation in the value of food units should occur when food comes in large packages which are acquired nonsynchronously across individuals. Therefore, if an individual acquires a large package of food, a fraction of that package should be less valuable to him than it is to an individual who has no food. The acquirer will then achieve a net fitness benefit if he can exchange that fraction of the food resource for an equivalent fraction at another point in time when he has little or no food. This leads us to the second condition.

There is no a priori reason an individual who is given food should reciprocate. In fact, from a selection point of view, individuals who do not reciprocate will be favored unless not doing so has some cost. This situation has been formally modeled by Axelrod and Hamilton (1981). Using the prisoner's dilemma as their test case, they find that the probability of future interactions between players determines whether cheating or reciprocating yields the highest fitness payoff.

This implies that reciprocity should not, from a selection point of view, be seen as a form of "payback." The cost of giving now is weighed against the benefit of receiving in the future, and giving now is not payback for past benefits but an attempt to increase the probability of receiving in the future. Individuals should therefore discriminate between those who have and have not given in the past not because of indebtedness but because of the probability of receiving in the future. Individuals who gave in the past should be more likely to give in the future, and, by giving now, the individual should be more likely to receive in the future by communicating that he gives to those who give.³

Whether this form of reciprocity exists among nonhumans has not yet been ascertained (see, however, Packer [1977] for evidence which suggests that reciprocity can occur among baboons in contests over mates and dominance status and Trivers [1972] for examples of interspecific reciprocity). Helping at the nest among some birds may also involve reciprocal altruism. Not all instances of food sharing and nest helping involve close kin. For example, unrelated helpers are reported for the green woodhoopoe (Ligon and Ligon 1978). In fact, some unrelated helpers have been observed to provide more food than helpers who are the siblings of the immature birds.

One proposal is that helpers directly benefit from remaining in the territory of breeding individuals, either by reducing their risk of being preyed upon or wounded in intraspecific competitive struggles or by obtaining access to high-quality feeding patches (Ligon 1983). This does not, of course, explain why helpers feed the young of the breeding pair unless the breeding

³ The actual proximate psychological mechanisms by which individuals "decide upon" alternative behavioral options may be more or less complex than this. The important point for the purposes of this discussion is that selection will favor reciprocal food sharing only if the giving of food affects the probability of receiving food in the future.

adults who are generally dominant to helpers permit access to the territory only to individuals who feed their offspring. This, then, would imply some form of trade or reciprocity. Another hypothesis which invokes reciprocal altruism is that helpers, by helping, increase their probability of obtaining helpers in the future when they are able to secure their own territory (Ligon 1983). However, this hypothesis is problematic because there seems to be no penalty associated with nonreciprocation. After being fed and cared for, birds which have been helped appear to have nothing to gain by returning the favor.

The nursing of sisters' offspring by female lions, elephants, and some pinnipeds (see Reidman 1982 for a review) is another possible candidate. The question remains: does kin selection or reciprocal altruism account for the evolution of this form of behavior? The fact that this class of food sharing is generally found among close kin does not necessarily imply kin selection. Kin selection requires that benefits to sister's offspring must be at least four times ($1/r$) as great as the cost to the giver. Selection for reciprocal altruism requires only that the costs of giving at time t be lower than the benefits of the giver's offspring's being fed at time $t + 1$. This could occur if the cost to the female of nursing several young (including both her offspring and sister's offspring) is lower than that of nursing her own offspring on two separate occasions. This should be the case if nursing is competitive with foraging. If lionesses took turns remaining with cubs and foraging, each might be able to raise more offspring than if each exclusively cared for and nursed her own offspring. This possibility has not, to my knowledge, been tested.

Even if this is the case, the question remains why this pattern is most prevalent among groups in which females are closely related. This is a complex problem. Other things being equal, close kin should be more likely to reciprocate than non-kin. This should be the case because cheating will have indirect fitness costs if the individual being cheated is closely related to the cheater. At the same time, related individuals may be more tolerant of cheating than unrelated individuals. This implies that kin selection and reciprocal altruism could interact in the evolution of this behavior. Unfortunately, very little is known about how kin selection operates when individuals who are equally related differ in other ways (such as reproductive potential or value as a partner in reciprocity) that might affect the costs and benefits associated with assistance giving. Modeling phenomena of this nature has proven difficult and cumbersome (see, for example, Charlesworth and Charnov's 1981 attempt to model kin selection in age-structured populations).

Similar problems occur when adult-adult food sharing is considered. Kin selection, tolerated theft, and tit-for-tat reciprocity all predict that large package size and nonsynchrony of acquisition should affect the costs and benefits of sharing. However, the above discussion indicates that differences in the value of resources to the individuals concerned must be greater for kin selection to favor sharing than for either tolerated theft or reciprocity. This suggests that the latter two forms of selection may be more directly involved in the evolution of adult-adult food sharing than kin selection but that kin selection may determine who is most likely to share with whom.

2. In "trade," resources in different fitness currencies are exchanged. Trade may be immediate or time-delayed. The suggestion (Ligon 1983) that subadult birds are feeding the offspring of other birds in exchange for access to high-quality territories is an example of immediate trade, in which provisioning and access occur simultaneously. In this case, there is no possibility of cheating in the sense of not reciprocating, because both resources are being given at the same time. Male-female meat sharing among chimpanzees may be one example of time-delayed trade among nonhuman animals. Teleki (1973) observed that male chimpanzees are more likely to share meat with estrous females and that they frequently mate with them after having given them the food. Males may therefore be

trading meat for future sex (although copulation frequently occurs immediately after the food is given). Another possible form of time-delayed trade may involve cooperation in the acquisition of food.

Cooperative acquisition. There are numerous reports which suggest that social carnivores such as lions, wolves, hyenas, and African hunting dogs hunt cooperatively in order to increase their chances of obtaining prey (Estes and Goddard 1967, Kleiman and Eisenberg 1973, Mech 1970, Schaller 1972). The same has been said of hunting among baboons and chimpanzees (Strum 1981, Teleki 1973). It has also been suggested that food is shared among these groups of organisms so that individuals will cooperate in the hunt. Given the foregoing discussion, we must ask why individuals should share food once the cooperation has already been secured. If reciprocal altruism is selecting for sharing, then it would seem that individuals who share are exchanging food for *future* cooperation. The cost of not reciprocating (i.e., sharing) is a function of its effects upon cooperation in the future. Whether this form of reciprocity is involved in sharing and cooperative hunting remains to be tested. If, however, tolerated theft can account for the presence of food sharing among social carnivores and primates (when they obtain large packages), reciprocity need not be involved. If an individual's share of a kill is simply a function of resource-holding potential (i.e., the degree to which an individual can monopolize a share of the kill through force), the number of individuals present, and the amount acquired, then individuals might cooperate simply to increase the amount acquired rather than because cooperation is a *sine qua non* of being shared with. The fact that old female hyenas and hunting dogs consume parts of kills but are generally too slow to participate in making kills is consistent with this interpretation.

From the above discussion, it is evident that a number of different hypotheses have been advanced to explain the evolution of food sharing and other forms of assistance giving, some of which are competing and some of which are applicable to distinct classes of food sharing. (For example, tolerated theft is clearly not applicable to most cases of sharing between parents and offspring [unless one concedes that parents share because the cost of listening to their children cry and whine is greater than the benefit of keeping the food].)

The data reviewed also indicate that animal behavior may be extremely variable and complex. Moreover, the intraspecific variation observed in food sharing (for example, white-fronted bee-eaters provision the offspring of other birds only when their brood has failed) suggests that learning is probably involved in much of it. Nevertheless, students of nonhuman animal behavior have made steady progress in understanding variation in food sharing and assistance giving using cost/benefit models derived from evolutionary theory. The extent to which these models will be useful in predicting variation in human behavior remains an open question and is a principal focus of this paper. The question here is not whether genetic variability among human groups determines variation in food sharing but rather whether we can account for much of the variation in human sharing patterns if we expect people to learn to adopt different behavioral patterns in different ecological contexts so that their behavior, on the whole, maximizes their inclusive fitness.

THE HUMAN CASE

Relative to other primates, parental provisioning of young among humans is exceptional in terms of both length and intensity. Human infants are likewise more altricial than other primates, although they are unexceptional relative to the Mammalia in general (Eisenberg 1982). Most dramatic, however, is the high level of *paternal* provisioning of young among human groups. While relatively high levels of male parental

investment are not unknown among nonhuman primates (such as the monogamous callithricids), human males represent an extreme in the continuum of male parental investment. Accounting for the origins and subsequent maintenance of a high level of male parental investment is an extremely interesting problem, but it will not be addressed in this paper.

Humans are also reported to share their food widely across the boundaries of the nuclear family, particularly in hunting and gathering societies (although, as mentioned above, there is also significant cross-cultural variation here). In addition, it is generally believed that people are far more likely to share with close kin than with other members of the population (see, for example, Sahlins 1972). While this generalization is consistent with the possibility that kin selection is involved in adult-adult food sharing, there is some controversy over whether "social" or biological kinship best explains the occurrence of this and related forms of behavior (see, for example, Chagnon 1979, 1980; Hawkes 1983; and Sahlins 1976 for contrasting positions).⁴ Moreover, as mentioned above, that people preferentially share with close kin does not necessarily mean that kin selection is the critical determinant of its occurrence.

Tolerated theft has also been recently advanced as an explanation of human adult-adult food sharing, particularly with respect to its original evolution in ancestral populations (Blurton Jones n.d.). The dramatic difference between the diets of human hunter-gatherers and other primates, particularly with respect to the meat component (Hill 1982, Butynski 1982), is critical here. Mean package size is larger, and, because hunting success is probably more variable than plant-food collection, acquisition should be less synchronous across individuals. In general, ethnographic reports suggest that meat is shared more extensively than plant foods (Bose 1964, Lee 1979, Morris 1982, Tanaka 1980).

This contrast between the diets of human hunter-gatherers and those of other primates has been invoked when reciprocity is offered as a possible explanation for the pervasiveness of food sharing among hunter-gatherers. The fact that game comes in large packages and that hunting success is sporadic suggests that individuals will share food when they have a "surplus" so that they will be shared with when they have little or none (Cashdan 1982, Coon 1971, Feinman 1979, Gould 1981, Lee 1979, Service 1966, Washburn and Lancaster 1968).

Clearly, there are parallel trends among anthropologists and evolutionary biologists in attempting to understand the occurrence of food sharing. Anthropologists, however, have not traditionally viewed food sharing and reciprocity in terms of individual fitness. Group-level and individual fitness are generally not distinguished.

One example of this mixture of individual and group-level models is Harris's (1979, 1980) treatment of reciprocity. Consistent with ethnographic generalization concerning the character of exchange in pre-state societies, Harris (1980:228), along with many other anthropologists (e.g., Sahlins 1972), defines reciprocity differently than do theoretical biologists: "There is (1) no immediate return, (2) no systematic calculation of the value of the services and products exchanged, and (3) an overt denial that a balance is being calculated or that the balance must come out even." According to Harris, this form of exchange might occur in hunting and gathering societies because, in addition to reducing the risk of having no food as a result of encounter luck in hunting, it negates the potential

⁴ The most parsimonious position is that social kinship is a direct derivative of genetic relatedness. Many of the heralded discontinuities between the two are probably the result of the fact that reciprocity and kinship are closely connected in human societies, partners in reciprocity often being classed as kin. However, the debate is more complex than this and is beyond the scope of the present discussion.

reward associated with the intensification of labor. With reciprocity as defined above, high producers receive no more than low producers in the form of either goods or prestige. Since, according to Harris, most hunter-gatherers are in constant danger of overexploiting their resources, rewarding intensification of labor would not be adaptive for the group.

If, as Harris argues, reciprocity in hunting and gathering societies represents an adaptation to the danger of overexploiting game resources, then it might be argued that this form of food sharing should not occur when there is no immediate danger of game depletion. Moreover, hunter-gatherers who share their food in a manner characterized by "reciprocity" as defined above should adopt other patterns of behavior which reflect an attempt to conserve resources. These are testable predictions.

The predictions of the various hypotheses offered to explain the evolution of adult-adult food sharing among humans are as follows:

The kin-selection hypothesis entails two predictions: (1) other things being equal, food sharing will occur most frequently between very close kin; and (2) the benefit to kin of shared food divided by the cost to the giver should be greater than the reciprocal of the genetic relatedness between the giver and the receiver.

The tolerated-theft hypothesis entails the following predictions: (1) food will be shared only to the extent that the cost of defending it is greater than the cost of keeping it; (2) other things being equal, differences in resource-holding potential will predict asymmetries in resource distribution; and (3) large packages that are nonsynchronously acquired will be shared more than small ones synchronously acquired.⁵

The hypothesis of tit-for-tat reciprocity predicts that (1) the cost of giving a unit of food at time t will be lower than the benefits of receiving an equivalent unit of food at time $t + 1$; (2) the net positive fitness gains from reciprocal food sharing will be greater than the initial costs of distinguishing reciprocators from nonreciprocators (i.e., the frequency of net beneficial instances of food sharing must be great enough to offset the initial costs associated with giving food to nonreciprocators who will then be excluded from future sharing interactions); (3) as with tolerated theft, large packages that are nonsynchronously acquired will be shared more than small ones synchronously acquired.

The cooperative-acquisition hypothesis predicts that (1) cooperatively acquired foodstuffs will be shared more than foods which are solitarily acquired and (2) individuals who cooperate in the acquisition of a resource will consume more of that resource.

Finally, Harris's conservation hypothesis implies that (1) resources will be shared without calculation of a balance when they are in danger of overexploitation and (2) this form of food sharing will be accompanied by other behavioral strategies that reflect an attempt to conserve resources.

To the extent that it is possible, these predictions will be tested against data on food sharing and resource acquisition among Ache hunter-gatherers in eastern Paraguay.

EMPIRICAL TESTS

This research, as we reported last year in these pages (Kaplan et al. 1984), was conducted with the Northern Ache of lowland

⁵ It is possible that factors other than package size and synchrony of acquisition across individuals affect the costs and benefits associated with defense and theft of resources. Also, in contrast with the second prediction listed for the tolerated-theft hypothesis, Blurton Jones (n.d.) explicitly argues that, as asymmetries in resource value become sufficiently large, resource-holding potential should become less important in determining the distribution of food resources.

subtropical eastern Paraguay.⁶ Full-time foragers until the last decade, they now combine foraging with swidden agriculture in settled mission communities, with most individuals still foraging for up to two weeks a month away from the mission. The data presented here were collected on nine foraging trips, ranging from 7 to 15 days in length, between October 1981 and May 1982. The foraging bands included 15–28 persons, with the mean numbers of adult males, adult females, and children being 9.6, 6.6, and 9.0 respectively. In all, these data represent 81 band days of forest subsistence.

The foraging and sharing pattern we observed was almost identical to informant reports on precontact life and that observed by Hill (n.d.) in 1978 at Manduvi, where foraging was virtually the only occupation. On Ache foraging trips, daily subsistence goals organize behavior. Foraging bands are highly mobile, remaining at a single campsite for one to four days. Game items are responsible for 60–80% of the calories Ache foragers consume. Honey is calorically the second most important resource, followed by an array of fruits, palm products, and insect larvae (Hawkes, Hill, and O'Connell 1982, Hill and Hawkes 1983, Hill et al. 1984). Virtually no food storage is practiced—the bulk of all food is consumed within 24 hours of acquisition. Food, once acquired, is shared throughout the band.

Two or three investigators accompanied the Ache on the foraging trips sampled. Virtually all resources acquired were weighed, counted, or measured. Caloric values were calculated using the *Handbook of Latin American Foods*, U.S. Department of Agriculture *Handbooks* 8 and 456, and analyses performed by the Ford Chemical Laboratory of Salt Lake City. Food consumption was monitored by (1) recording an entire day's activities relating to food acquisition and consumption of a single adult, randomly selected (without replacement); (2) recording the activities of all persons in observation distance every ten minutes throughout the day; (3) recording all the consumers of a particular food; and, finally, (4) dividing the campsite into regions and recording all the consumption activities of the individuals located in each. Whatever the sampling technique, an attempt was made to record, for every consumption event observed, (1) the consumer, (2) the resource type (monkey, armadillo, palm fruit, etc.), (3) the original acquirer of the resource being consumed, and (4) where possible, the amount by visual estimate. These combined techniques yielded a total of 6,923 consumption-event entries.⁷

All analyses reported here were performed by calculating relative frequencies of consumption events. To determine whether relative frequencies of consumption accurately reflected relative amounts of calories, we performed three independent tests on the data (see Kaplan et al. 1984:113) and found (1) a high correlation between the total calories acquired of each resource type (monkey, armadillo, etc.) and the total number of consumption events recorded for that resource; (2) a high correlation between the total calories acquired by each adult forager and the total number of times he/she was coded as the acquirer of a resource being consumed; and (3) no significant difference between the amount consumed by women when their spouses were the acquirers and that consumed by them when men other than their spouses were the acquirers. Together these tests indicated that no resources or acquirers were selectively over- or underrepresented by our sampling procedure and that frequencies of consumption events are a valid, unbiased index of quantity in calories.

⁶ A detailed description of the methods employed in this research may be found in Kaplan (1983) and Hill (1983).

⁷ A "consumption event" is a single entry generated by one of the sampling methods just described. For an entry to qualify as a consumption event, the consumer, the acquirer, and the species of the foodstuff must have been recorded.

We may now ask whether the predictions outlined above can be appropriately tested by observing behavior on foraging trips. Would the mission attachment of Ache foragers vitiate the tests? If the foragers had stores of food at the mission (as, in essence, they do) and if foraging trips were of such short duration that stored food at the mission dampened temporal fluctuations in the acquisition of jungle foods, then the pattern of resource acquisition in the jungle would not predict food sharing. However, all the foraging trips we monitored lasted at least seven days. All food brought from the mission was eaten within the first day or two and accounted for no more than 5% of the total calories consumed. In addition, as we have said, food acquired on jungle foraging trips is not stored for later consumption. If the giving and receiving of resources at the mission affected relationships between individuals in the jungle—for example, if individuals who gave a lot at the mission (such as those who had a special relationship to the missionaries and had privileged access to goods) were shared with in the jungle irrespective of their work effort or the amount of food they acquired—this would affect the “balance” of giving in the jungle but not the basic predictions of the hypotheses to be tested.

Given the large sample of consumption events, a kin bias in sharing, if it exists, should be detectable statistically even if other factors also affect who shares with whom. The prediction of the tolerated-theft and tit-for-tat-reciprocity models that resources which come in large packages and are nonsynchronously acquired across individuals will be shared most is unaffected by the possibility that mission relationships affect sharing in the jungle. The same is true of the prediction that cooperatively acquired food will be shared more than solitarily acquired resources. It is possible that the Ache are no longer concerned about the conservation of resources now that they can rely on mission foods, but this seems unlikely; more than 90% of the animal matter consumed by the Ache is derived from jungle foraging, and some important game species (such as peccaries) have been severely depleted near the mission (Hill and Hawkes 1983).

Table 1, a revised version of the one in our earlier report including additional data analyzed since its publication, presents the results of an analysis of food sharing in terms of classes of resources and relationship between acquirer and con-

TABLE 1
FOOD SHARING BY RESOURCE CLASS (PERCENT)

RESOURCE AND CONSUMER CLASS	ACQUIRER					
	N	Self	Spouse	Sibling	Parent	Other
Meat						
Men	1,376	5.7	0	6.8	0	87.5
Women	998	0	14.8	2.8	0	82.4
Children	787	0	0	0	16.9	83.1
Honey						
Men	454	16.5	.6	5.7	0	77.2
Women	408	2.5	14.7	1.5	0	81.4
Children	232	0	0	0	11.6	88.4
Collected						
Men	888	22.0	13.4	3.8	0	60.8
Women	959	39.4	6.5	1.6	0	52.5
Children	549	0	0	3.3	25.5	71.2
Mission-brought						
Men	85	0	40	0	0	60
Women	93	59.2	0	3.2	0	37.6
Children	94	0	0	0	50.0	50.0
Total						
Men	2,803	12.4	5.6	5.5	0	76.5
Women	2,458	18.0	11.0	2.1	0	68.9
Children	1,662	6.0	0	1.1	20.9	78.0
All	6,923	11.4	6.2	3.2	5.0	74.2

sumer. Two facts are immediately evident here: (1) The Ache receive a very high percentage of calories from individuals outside their nuclear families, and (2) meat is shared most, followed closely by honey and then by other collected and mission-brought resources.

Table 2 presents a more detailed breakdown of sharing by food type. Meat, honey, and collected resources do not overlap in the amount shared outside the nuclear family. A Kruskal-Wallis analysis of variance shows that there are no significant differences among the meat resources ($HC = 7.0, p = .43, df = 7$) or among the different honeys ($HC = 0.39, p = .53, df = 1$). There are suggestive but nonsignificant differences among the collected resources ($HC = 10.2, p = .11, df = 6$); the range within this class is quite high. There are also highly significant differences between the three classes ($HC = 32.8, p < .000001, df = 2$).

The kin-selection hypothesis. The results of the test of the first prediction of the kin-selection hypothesis—that, other things being equal, close kin will be preferentially shared with—have already been reported (Kaplan et al. 1984). Briefly, for meat and honey, women, children, and the adult siblings of the acquirer receive no more from their husbands, fathers, and brothers, respectively, than would be expected by chance; in other words, individuals who are not closely related to the acquirer receive as much food from him as do his wife, children, and siblings. This is clearly inconsistent with the prediction. For other collected and mission-brought resources, in contrast, not only does each consumer class receive more food from every category of nuclear-family member who produces food than would be expected by chance, but the values are highly significant (particularly for mission-brought re-

TABLE 2
FOOD SHARING BY INDIVIDUAL RESOURCE

	% CONSUMED BY NUCLEAR FAMILY OF ACQUIRER	% CONSUMED BY INDIVIDUALS OUTSIDE NUCLEAR FAMILY OF ACQUIRER
Collected resources		
Palm fiber	31	69
Palm heart	28	72
Oranges	32	68
<i>Vivella (Campomanesia zanthocarpna)</i> ^a	92	8
<i>Kurilla (Rheedia brazilense)</i> ^a	77	23
Larvae	42	58
Miscellaneous ^b	36	64
Honey		
Honey (<i>Apis mellifera</i>)	15	85
Miscellaneous ^b	19	81
Meat		
Collared peccary	11	89
White-lipped peccary	11	89
Armadillo	9	91
Monkey	10	90
Paca	5	95
Deer	6	94
Coati	9	91
Miscellaneous ^b	13	87

^a No English name known.

^b Includes items taken in quantities too small for obtaining accurate sharing measures. Miscellaneous collected resources include mostly fruits; miscellaneous honey includes all honey produced by bees other than *Apis mellifera*; miscellaneous meat includes birds, fish, and other animal species taken rarely.

sources [$p < .00001$]). The adult siblings of the acquirer, however, do not receive preferential shares. The simple nuclear family of parents and offspring therefore appears to be a unit of consumption. This result is consistent with the expectation that kin-selected food sharing will be most likely to occur between adults and immature individuals.

The cooperative-acquisition hypothesis. While no game species is exclusively acquired cooperatively or hunted solitarily, two classes can be isolated in terms of the importance of cooperation in acquisition. Deer, armadillos, and collared peccaries are almost always acquired by single hunters, whereas white-lipped peccaries, pacas, and monkeys are generally hunted by cooperative pursuit groups (although the precise frequencies of cooperative and solitary acquisition have not yet been tabulated). The Kruskal-Wallis test showed no differences in sharing pattern between these two groups of resources ($HC = .01, p = .91, df = 1$). The mean percentage of food shared outside the nuclear family of the acquirer was 92% for the solitarily acquired resources and 91% for the cooperatively acquired resources. These results imply that cooperative acquisition is not a necessary condition for food sharing and that other factors must be involved in determining the variation in the extent to which resources are shared. They do not, however, imply that cooperative acquisition is not a sufficient condition for food sharing—this is not testable with the Ache data. Other social contexts in which little sharing occurs but some foods are cooperatively acquired would be more appropriate for such a test.

The tolerated-theft and tit-for-tat-reciprocity hypotheses. To determine whether the differences in sharing between resource classes were associated with differences in package size and synchrony of acquisition across individuals—thus satisfying the predictions of both tolerated-theft and tit-for-tat-reciprocity hypotheses—we obtained measures of the two independent variables. Package size was defined as the mean number of calories acquired of a resource at any one time. The measure of acquisition synchrony was mean standard deviation across families in the amount of each resource acquired on each day.

This last measure requires some explanation. As mentioned above, the total number of calories acquired by each individual of each resource was recorded for each foraging day sampled. However, given the division of labor (women collect wild foods while men hunt) and given the fact that food (particularly meat and honey) tends to be distributed to nuclear families, we reasoned that the best measure of synchrony of acquisition would be between families rather than between individuals. We tabulated the total amount acquired of each resource by each family on every foraging day sampled (single individuals without spouses were counted as families as well). With these measures, we then calculated the standard deviation of the mean across families for each resource on each day sampled. This generated a day-by-day measure of acquisition synchrony (the higher the standard deviation the less synchronized were families in the acquisition of that resource). We then calculated the mean standard deviation for each resource both per trip and for all days sampled.

Table 3 displays the total amount acquired, the mean package size in calories, and the mean standard deviation across families per day for each of the three resource classes. There are clear differences among the three classes in both standard deviation across families and package size as well as in the total amount acquired. When the amount shared was regressed on log-transforms of each of the predictor variables, the standard-deviation and package-size measures, as expected, best predicted sharing. The standard-deviation measure accounted for some 61% of the variance in food sharing ($r = .78, r^2 = .61, p < .000001, N = 27$). Package size in calories predicted 45% of the variance ($r = .67, r^2 = .45, p < .0001$). Total calories acquired also significantly predicted sharing but ac-

TABLE 3
TOTAL AMOUNT ACQUIRED, PACKAGE SIZE, AND ACQUISITION
VARIANCE BY RESOURCE CLASS

RESOURCE TYPE AND TRIP	MEAN DAILY CALORIES ACQUIRED BY THE BAND	MEAN PACKAGE SIZE (CAL.)	DAILY MEAN STANDARD DEVIATION ACROSS FAMILIES
Collected resources			
1	6,596	814	977
2	15,000	921	1,753
3	20,505	758	2,481
4	5,842	880	1,146
5	28,762	1,286	2,857
6	11,052	1,309	2,116
7	27,287	1,756	4,806
8	8,734	687	1,491
9	30,475	1,649	2,923
Overall	17,139	1,118	2,283
Honey			
1	28,388	25,020	9,472
2	38,875	5,611	10,412
3	6,566	1,624	3,119
4	22,387	5,197	12,501
5	9,800	3,067	3,625
6	8,117	3,865	4,286
7	29,368	7,887	10,555
8	12,174	2,867	7,866
9	5,277	3,518	4,026
Overall	17,874	6,517	7,318
Meat			
1	54,692	2,143	5,241
2	72,674	2,752	11,427
3	55,922	2,540	13,723
4	42,384	2,325	9,483
5	49,260	2,208	7,191
6	41,516	2,339	12,116
7	43,626	2,487	6,280
8	25,521	1,821	5,807
9	57,901	4,033	9,900
Overall	49,277	2,516	9,019

counted for less of the variance than the above two measures ($r = .57, r^2 = .33, p = .002$).

To test the predictive value of standard deviation and package size further, we treated each resource separately. We also obtained a second measure of package size (in kilos as opposed to calories) to determine whether weight or calories best predicted sharing. Tables 4–7 display mean calories acquired per day, mean package size in calories, mean package size in kilos, and mean standard deviation across families. Regressions were again performed on the data, using the overall means for each of the 17 resources the Ache take in large enough quantities to permit reliable measures. A similar pattern of results emerged from this analysis. Both standard deviation and package size significantly predicted variation in the extent to which resources are shared. Package size predicted 54% of the variance ($r = .74, r^2 = .54, p < .001, N = 17$) and standard deviation 27% ($r = .51, r^2 = .27, p < .05$). Package size in calories is a much better predictor than package size in kilos, which predicted only 23% of the variance ($r = .48, r^2 = .23, p = .18$ [ns]). This implies that caloric content rather than mass is the important feature of package size in patterning food sharing. These results conform to the predictions of the tit-for-tat-reciprocity and tolerated-theft hypotheses.

Several features of the Ache sharing pattern are, however, inconsistent with the tolerated-theft hypothesis. First, hunters eat from their own kills significantly less than other individuals (Kaplan et al. 1984). The tolerated-theft hypothesis is based upon the premise that sharing is the result of contests over

TABLE 4
MEAN CALORIES ACQUIRED PER DAY PER TRIP BY THE ENTIRE BAND

RESOURCE	TRIP									Overall
	1	2	3	4	5	6	7	8	9	
Collected resources										
Palm fiber	4,394	9,314	4,945	4,606	7,276	7,459	16,674	2,108	5,879	7,734
Palm heart	1,642	1,501	947	549	722	852	2,202	937	1,834	1,243
Oranges	0	0	0	0	0	0	321	602	20,929	2,428
Virella	0	0	9,535	0	0	0	0	0	0	1,059
Kurilla	0	0	0	0	13,890	0	0	0	0	1,543
Larvae	281	3,825	377	216	1,599	117	2,884	2,811	1,825	1,548
Miscellaneous	9	267	4,702	478	2,436	2,630	1,836	690	9	1,451
Honey										
Honey	27,624	35,821	6,339	20,044	6,785	5,878	24,131	11,034	4,810	13,057
Miscellaneous	763	3,054	202	2,343	5,511	2,239	5,237	1,103	468	2,324
Meat										
Collared peccary	162	0	3,105	4,258	0	15,876	0	3,446	7,452	2,541
White-lipped peccary	0	21,338	29,340	17,126	9,489	7,322	0	0	9,040	10,406
Armadillo	6,677	4,775	5,948	1,419	11,123	2,457	15,648	6,274	16,655	7,886
Monkey	19,332	14,623	1,104	8,086	12,000	5,450	12,055	6,339	12,384	10,153
Paca	10,265	28,281	540	1,736	14,666	3,434	5,929	2,259	4,860	7,997
Deer	7,978	0	8,018	5,319	0	3,373	2,225	1,842	4,216	3,663
Coati	6,445	3,252	994	2,888	0	1,814	5,508	3,903	2,155	2,995
Miscellaneous	3,834	405	6,817	1,522	1,981	1,789	2,261	1,459	1,140	2,356

TABLE 5
MEAN PACKAGE SIZE IN CALORIES

RESOURCE	TRIP									Overall
	1	2	3	4	5	6	7	8	9	
Collected resources										
Palm fiber	2,681	1,305	2,618	1,948	2,995	3,729	4,061	2,898	3,919	2,906
Palm heart	353	318	323	297	297	351	749	402	681	419
Oranges	0	0	0	0	0	0	1,795	2,188	20,929	8,304
Virella	0	0	312	0	0	0	0	0	0	312
Kurilla	0	0	0	0	1,355	0	0	0	0	1,355
Larvae	288	200	164	252	198	388	771	638	1,186	454
Miscellaneous	17	333	1,427	612	658	930	1,809	569	42	6,397
Honey										
Honey	26,987	9,803	8,951	33,734	4,634	11,757	23,685	13,873	12,024	16,161
Miscellaneous	5,344	3,245	476	3,226	4,732	4,478	11,222	1,837	1,559	4,013
Meat										
Collared peccary	1,134	0	27,945	29,808	0	29,970	0	16,767	37,260	23,814
White-lipped peccary	0	28,463	66,015	59,940	22,140	35,100	0	0	45,333	42,832
Armadillo	4,042	2,724	4,027	4,354	5,200	4,698	6,024	5,685	6,133	4,765
Monkey	2,849	3,102	2,967	2,879	3,178	4,193	2,593	3,032	2,903	3,077
Paca	10,265	10,419	4,860	12,150	12,834	11,448	8,505	11,745	12,150	10,846
Deer	27,922	0	36,080	37,230	0	16,863	33,371	20,258	42,158	30,555
Coati	4,512	7,587	8,942	5,054	0	6,669	5,170	6,095	7,182	6,401
Miscellaneous	1,677	315	2,578	1,442	1,685	2,016	2,269	3,209	971	1,796

food. According to this hypothesis, individuals weigh the costs of defending some portion of what they acquire against the benefits of keeping it. Therefore, they should never give up so much food that its value is greater to them than it is to the thieves. However, this is exactly what occurs when hunters eat less from their own kills than other band members. Moreover, if hunters were concerned about meat's being stolen from them, they would eat as much of the kill as they could before others arrived; instead, they save it for consumption by the entire band at the end of the day. Also inconsistent with the tolerated-theft hypothesis is the fact that food is often saved for individuals (both men and women) even when they are not present when others are eating. In addition, a man who finds honey will sometimes call for another man to chop the tree to extract it so that he can continue hunting. Although he will

receive a share of the honey later in the day, he will miss out on the consumption when it is first extracted from the tree. This is especially interesting in light of the fact that he will eat less of the game he acquires than other band members. Finally, I see no evidence that resource-holding potential has any effect on food sharing. Informants report that there is a great deal of variation among Ache men in fighting ability, but, as far as we could tell, these differences were not reflected in the distribution of food. Moreover, women and adolescent males were shared with whether or not they were accompanied by close adult male kin (or a spouse).

The question of whether the data are consistent with tit-for-tat reciprocity is more complex. In order to determine whether the benefits of food sharing for individual Ache at time $t + 1$ actually exceeded its costs at time t , we developed a simple

TABLE 6
MEAN PACKAGE SIZE IN KILOGRAMS

RESOURCE	TRIP									Overall
	1	2	3	4	5	6	7	8	9	
Collected ^a										
Palm fiber	7.98	3.88	7.79	5.8	8.91	11.1	12.09	8.62	11.66	8.65
Palm heart	.59	.53	.54	.50	.50	.59	1.26	.68	1.14	6.33
Oranges	0	0	0	0	0	0	6.0	2.03	6.04	4.69
Virella	0	0	.44	0	0	0	0	0	0	.44
Kurilla	0	0	0	0	3.27	0	0	0	0	3.27
Larvae	.1	.07	.06	.09	.07	.14	.27	.22	.41	.16
Honey										
Honey	9.87	3.59	3.28	12.34	1.7	4.3	8.67	5.08	4.4	5.91
Miscellaneous	1.96	1.19	.17	1.18	1.73	1.64	4.11	.67	.57	1.47
Meat										
Collared peccary	.7	0	17.25	18.4	0	18.5	0	10.35	23.0	14.70
White-lipped peccary	0	17.57	40.75	37.0	13.67	21.67	0	0	27.98	26.44
Armadillo	3.13	2.11	3.12	3.38	4.03	3.64	4.67	4.41	4.75	3.69
Monkey	2.21	2.4	2.3	2.23	2.46	3.25	2.01	2.35	2.25	2.38
Paca	6.34	6.43	3.0	7.5	7.92	7.07	5.25	7.25	7.50	6.47
Deer	25.0	0	32.95	34.0	0	15.4	30.48	18.5	38.5	27.83
Coati	2.78	4.68	5.52	3.12	0	4.12	3.19	3.76	4.43	3.95
Miscellaneous	1.16	.22	1.78	.99	1.16	1.39	1.56	2.21	.7	1.24

^a Values for miscellaneous collected resources were not calculated because package size in kilograms varied considerably across those resources.

TABLE 7
MEAN DAILY STANDARD DEVIATION ACROSS FAMILIES

RESOURCE	TRIP									Overall
	1	2	3	4	5	6	7	8	9	
Collected										
Palm fiber	786	1,368	960	2,374	1,809	2,251	4,399	2,246	1,817	2,001
Palm heart	271	258	201	285	221	315	421	403	568	327
Oranges	0	0	0	0	0	0	712	502	2,878	1,364
Virella	0	0	1,308	0	0	0	0	0	0	1,308
Kurilla	0	0	0	0	2,158	0	0	0	0	2,158
Larvae	182	1,389	158	300	790	205	711	1,108	728	619
Miscellaneous	9	139	2,762	371	571	1,039	1,491	453	14	761
Honey										
Honey	9,244	9,863	3,070	23,125	2,613	7,060	9,858	7,586	3,805	8,469
Miscellaneous	1,611	1,285	302	1,681	3,787	1,828	5,213	1,513	740	1,996
Meat										
Collared peccary	342	0	9,315	12,169	0	16,570	0	7,164	23,565	11,521
White-lipped peccary	0	12,872	27,844	31,223	9,949	14,947	0	0	19,338	19,362
Armadillo	2,477	2,912	2,360	2,028	2,862	2,007	4,266	2,630	3,497	2,782
Monkey	2,563	2,661	1,104	3,392	2,428	2,132	3,267	2,402	3,508	2,606
Paca	3,815	6,986	1,620	4,960	6,616	4,674	4,094	3,130	3,842	3,919
Deer	8,419	0	12,027	15,199	0	6,884	11,124	7,657	13,332	10,663
Coati	2,199	980	2,981	3,422	0	4,685	4,299	2,933	4,578	3,260
Miscellaneous	1,026	116	1,799	762	768	1,082	1,441	1,502	736	1,026

model of the relationship between nutritional status (as a component of fitness) and quantity of food available for consumption. Since the mean number of children per couple on the foraging trips we sampled was approximately 1 (.9, actually), we estimated that the most a family could consume in a day would be approximately 12,500 calories (5,000 calories for each adult and 2,500 for the child). Assuming that food would spoil within approximately 24 hours of its acquisition (two days appears to be the maximum for meat in the jungle), any amount over 12,500 calories acquired on one day would be of little or no value to the family that acquired it if it were not shared. Similarly, we calculated that a single man or woman without children could utilize only 5,000 calories on any one day and a single adult with a child some 7,500 calories. Figure 2 represents these assumptions: nutritional status is shown as a func-

tion of the amount of food available for consumption. According to the simplistic assumptions of this model, each increment in food confers an equal increment in nutritional status until the point is reached where additional units of food are of no value (a more gradually sloped diminishing-returns curve would probably be more realistic, but for the purposes of simplicity we have chosen this one as an initial approximation).

With this model, we then calculated the nutritional status of Ache families and single individuals with and without band-level sharing. On each day, every family was given different scores on the basis of five variant conditions: (1) no sharing; (2) sharing all resources equally; (3) sharing only meat; (4) sharing only honey; and (5) sharing only collected items. They were awarded equal increments up to 125 points, when their daily

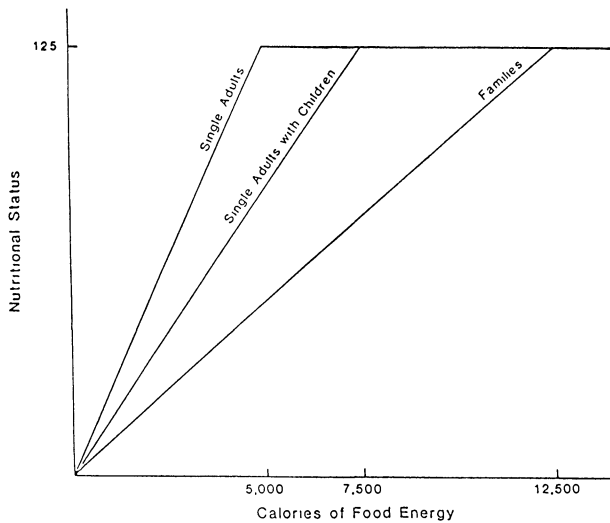


FIG. 2. Nutritional status in relation to amount of food available for consumption.

maximum was reached (12,500, 5,000, 7,500 calories for families, single adults, and single adults with children, respectively). The results of this analysis are displayed in table 8. In all cases, the lowest score is for "no sharing." For families, sharing of collected items only did not increase this score (probably because sharing increased nutritional status at times and decreased it at others). Sharing of honey alone increased nutritional status by 20%, whereas sharing of meat alone increased nutritional status by a full 40%. Sharing of all food provided an 80% increase in nutritional status. This is consistent with the observed pattern, in which meat is shared most, followed by honey and then by other collected items. In all but 4 of the 56 families examined, sharing of all foods increased nutritional status, and in the 4 cases in which sharing reduced nutritional status the reduction was slight (10–30%). Interestingly, 3 of

TABLE 8
SHARING AND NUTRITIONAL STATUS

	NUTRITIONAL STATUS RAW SCORE	% INCREASE FROM NO SHARING
Couples ($N = 56$)		
No sharing	62.7	...
Sharing collected foods only	63.5	0
Sharing honey only	70.7	20
Sharing meat only	80.6	40
Sharing all foods	96.9	80
Single males ($N = 16$)		
No sharing	66.0	...
Sharing collected foods only	73.9	20
Sharing honey only	80.2	30
Sharing meat only	70.9	20
Sharing all foods	104.0	80
Single males with children ($N = 3$)		
No sharing	71.0	...
Sharing collected foods only	81.3	10
Sharing honey only	68.3	0
Sharing meat only	82.7	20
Sharing all foods	93.3	30
Single females with children ($N = 3$)		
No sharing	7.0	...
Sharing collected foods only	22.0	740
Sharing honey only	37.6	1,530
Sharing meat only	74.0	3,130
Sharing all foods	98.3	4,200

these 4 cases occurred on one foraging trip that included several adolescent couples (i.e., less than twenty years of age) who produced little food. These young couples benefitted a great deal from the sharing and, incidentally, were closely related to some of the older couples. Single males benefitted less from sharing than did couples because they tended to produce more than they consumed; single females benefitted by far the most, again because males produced approximately five times as much food as females.

This analysis points up some inconsistencies between the observed pattern of Ache food sharing and the tit-for-tat-reciprocity model. While almost all families and single individuals achieve higher nutritional status by the band-level sharing of resources than they would have by not sharing, some individuals benefit a great deal more than others. Although the mean increase in nutritional status is 80%, the standard deviation across families and individuals is quite high (102%) and the range is much greater (–30% to +570%). This is because some individuals and families produce more than others. Those who gain least from sharing both produce more and are more consistent in their production than others.

Variation in the extent to which people benefit from a band-level pooling of food is even more clearly demonstrated when this variation in food production is examined. This analysis shows that single men are the clear "losers" in the band-level pooling of food. The mean daily calories produced by single men is 6,086, whereas the same figure for families is 11,080. Since the mean number of children per family on foraging trips is approximately 1, the mean number of consumers for families is 2.5 (one adult male, one adult female, and one half for the child⁸). Thus, while families only produce 1.82 times as many calories as single males, they represent 2.5 times as many consumers. Moreover, these measures of central tendencies obscure much of the variation across individuals. A full 30% of the single males ($N = 17$) produce more calories by themselves than the mean for entire families. There is also a great deal of variation among families in their food acquisition. While the mean daily caloric production of families is 11,080, the standard deviation across families is 4,800. That is, after a mean of eight days of foraging, the standard deviation in total caloric production across families is 38,400 calories. In fact, we have observed as much as a sixfold difference between families in their caloric production over the course of a foraging trip.

Yet, in spite of this variation, there is no relationship between the amount of calories produced and the amount of food eaten (Pearson $r = .31$, $p = .12$, $N = 25$). In fact, the best predictor of the amount of food consumed by families is the number of children present ($r = .92$, $p < .000001$, $N = 25$)⁹. This is not surprising, since the data show that no individuals lost more than a kilo and a half of body weight during a foraging trip. Thus, all the data suggest that the Ache are pooling most of the food they acquire and are sharing food among families according to the number of dependents present.

⁸ Given the age distribution of the children who went on foraging trips, counting them as half-consumers seemed the most accurate approximation.

⁹ These last two tests were performed on the data obtained on trips 6–9 only, when scan sampling (reporting on everyone in sight every ten minutes) was used. This technique yields the most representative data when comparisons between individuals in food consumption are to be performed because of the number of data points it generates and, more important, because it samples all individuals to be compared at the same time. The tests were performed on normalized z-scores so that the data from separate trips could be meaningfully combined. Collected foods were the only resource class for which a significant positive correlation between amount acquired and amount consumed was found. This result is consistent with the fact that collected resources are shared less than meat or honey.

TABLE 9
LONG-TERM VARIATION IN MEAT PRODUCTION ACROSS FORAGERS

FORAGER PERSONAL ID NUMBER	MEAN DAILY MEAT CALORIES ACQUIRED, 1980	DAYS SAMPLED 1980	MEAN DAILY MEAT CALORIES ACQUIRED, 1981-82	DAYS SAMPLED 1981-82	MEAN DAILY MEAT CALORIES ACQUIRED OVERALL	TOTAL DAYS SAMPLED
0131.....	1,476	12	5,192	49	4,461	61
0003.....	6,111	28	7,896	26	6,970	54
0015.....	6,637	20	8,198	31	7,586	51
0051.....	10,296	14	8,966	35	9,346	49
0055.....	5,944	15	6,930	31	7,211	46
0009.....	10,472	14	8,443	31	9,074	45
0057.....	5,436	20	4,334	24	4,835	44
0165.....	3,954	28	5,726	16	4,599	44
0013.....	9,836	15	7,672	22	8,549	37
0159.....	9,473	28	5,252	7	8,628	35
0071.....	2,860	14	1,690	19	2,186	33
0099.....	13,539	12	7,715	20	9,899	32
0097.....	6,057	12	10,720	17	8,790	29
0045.....	4,774	10	3,263	15	3,867	25
0029.....	4,743	5	4,185	19	4,301	24
0069.....	3,026	17	5,495	7	3,746	24
0047.....	6,526	8	2,908	14	4,223	22

These results suggest that tit-for-tat reciprocity does not characterize the pattern of Ache food sharing, at least over the short term (i.e., during the course of an average eight-day foraging trip). Why do better-than-average producers give away more food than they receive? Why do they not keep more food for themselves? Or, alternatively, why do they not stop working when they have produced more calories than other individuals? In fact, the opposite is true: there is significant *positive* correlation between the number of meat calories men produce per hour (rate) and the number of hours they work (Hill and Hawkes 1983, Hill 1983).

One possible explanation is that, over the long term, food given is approximately equal to food received and that our measures do not include a long enough time span to observe the ultimate balance in the sharing of food. This would be the case if the only differences between families in the amount produced were due to the number of dependents present and to foraging "luck." If the principal reason families differed in the amount of calories they produced on trips were a function of encounter luck with large packages, then short-term differences in production would disappear over time. This is illustrated by the fact that a single peccary, which yields an average of 50-60,000 calories, raises mean daily production by some 7,000 calories over the course of an eight-day foraging trip.

There are data, however, which suggest that, in the long run, reciprocity will not be completely balanced. Data collected in 1980 by Hill and Hawkes, when compared with data collected by Hill, Hawkes, Hurtado, and Kaplan in 1981 and 1982, show consistent differences in production among hunters. For the 17 individuals for whom we have over 20 foraging days of data representing both field seasons, there is a significant correlation in the mean daily acquisition of meat between the two (Pearson $r = .54$, $p = .02$; see table 9). Moreover, the correlation progressively increases as the sample is reduced to include only individuals for whom we have 25, 30, 35, and 40 foraging days sampled. For the 8 individuals for whom we have over 40 foraging days sampled, the correlation in mean daily calories of meat acquired between the two field seasons is $.79$ ($p = .02$). Among these latter individuals, there is more than a twofold difference between the best and the worst hunters. It is therefore clear that there are real and consistent differences in production between individuals over the

long run.¹⁰ These differences between hunters must have been known to the Ache when they were foraging full-time in pre-contact days.

The conservation hypothesis. Although we did not specifically collect data to test the conservation hypothesis, there is some evidence inconsistent with its predictions. While the data we collected are consistent with reciprocity as Harris defines it, we could find no evidence that the Ache are concerned with the overexploitation of resources. In fact, the opposite is true.

First, if the Ache were attempting to conserve resources, they would selectively cull males from the game items they hunt and spare females and their offspring.¹¹ This is not the case. Females represent 48% of all adult animals taken. Moreover, when females are taken, so are their offspring. The only species for which the Ache attempt to cull males is *Cebus apella* (capuchin monkey), the most abundant of all game animals the Ache hunt. They report that they attempt to kill males because they are larger and provide more meat.

Another feature of their hunting pattern is that they not only kill and eat endangered species (in direct contrast to Ross's 1978 hypothesis) but destroy whole groups of them. On the third foraging trip we sampled, the Ache encountered a colony of bush dogs (*Speothos venaticus*) and systematically killed all of the animals present (three females and one male). Bush dogs are considered an endangered species by the World Wildlife Organization and are very rarely encountered in eastern Paraguay.

Again, the Ache frequently chop down fruiting trees rather than climb them and pick the fruits. They do this even in areas they frequently revisit. Similarly, unlike some other South American peoples such as the Kayapo, who take honey in such a way as to conserve the hive (Posey 1983), the Ache destroy the hives when they take honey.

¹⁰ Hill (personal communication) found that these differences are due to rate (calories acquired per hour foraged) rather than to the number of hours worked. These differences are probably therefore due to differences in skill.

¹¹ There are conditions under which the harvesting of females can increase productivity rather than decrease it. However, in most cases, the selective culling of males appears to be the solution of choice in maintaining game populations.

TABLE 10
PREDICTIONS AND RESULTS

HYPOTHESIS	PREDICTIONS	RESULTS		
		Untested	Supported	Unsupported
Kin selection	1. Food sharing between individuals should be inversely related to kinship distance.			X
	2. Benefit to kin of shared food divided by cost to giver should be greater than reciprocal of genetic relatedness between giver and receiver.	X		
Conservation	1. Resources in danger of overexploitation should be shared.			X ^a
	2. Foragers should attempt to conserve resources in danger of overexploitation.			X ^a
Cooperative acquisition	1. Cooperatively acquired resources should be shared more than solitary acquired ones.			X
	2. Those individuals who cooperate in the acquisition of a resource should consume more of that resource.			X
Tolerated theft	1. Food should be shared only to the extent that the cost of defending it is greater than the benefits of keeping it.			X
	2. Differences in resource-holding potential should predict asymmetries in the distribution of resources.			X ^a
	3. Large packages which are nonsynchronously acquired should be shared more than those which are small and synchronously acquired.		X	
Tit-for-tat reciprocity	1. The cost of giving a unit of food at time <i>t</i> should be lower than the benefits of receiving an equivalent unit at time <i>t</i> + 1.		X ^b	
	2. The net fitness gains from reciprocal food sharing must be greater than the initial costs of distinguishing reciprocators from nonreciprocators.	X		
	3. Large packages which are nonsynchronously acquired should be shared more than those which are small and synchronously acquired.		X	
	4. Individuals who give away more food should receive more food.			X

^a Prediction not tested quantitatively, but available evidence does not support prediction

^b Conclusion based upon suggestive evidence only

Lastly, in direct contrast with Harris's hypothesis, Ache hunters appear to be accorded the highest status for peccary kills. Peccaries are the game animals most in danger of overexploitation. In fact, they have been virtually wiped out within a day's walk of the mission. It appears very unlikely that the Ache share their food resources to prevent intensification of labor and overexploitation of food resources.

DISCUSSION

The predictions and results are summarized in table 10.

Kin selection. Within the band, close kin receive no more meat and honey from their acquirers than do more distantly related or unrelated individuals. Spouses and children do, however, receive more fruits, larvae, palm products, and mission-brought foods from their wives, husbands, and parents than do other band members. This result is consistent with the

above discussion of kin selection among nonhumans; kin-selected food sharing is most likely to occur with parental provisioning of offspring. This does not mean, however, that no kin bias exists in the sharing of even meat and honey when one considers the population of the Ache as whole rather than members of single foraging bands. It is possible that Ache foragers do, in fact, receive more food from their close kin than a random sharing pattern would predict, simply by virtue of their being more likely to live in the same band as their relatives. Even if the fitness benefits associated with tit-for-tat reciprocity are the most important determinants of the extent to which food is shared among different groups, there is still some reason to believe that, other things being equal, individuals will preferentially establish reciprocal relations with close kin whenever possible.

If this is true, the quantity and quality of close kin with whom one could potentially share food should determine whether reciprocal food sharing primarily involves genetically

related individuals (see Wasser 1982 for a related but more formal discussion of this issue). If the optimum number of reciprocal food-sharing partners exceeds the number of close kin with whom individuals live, the bias in favor of close kin should disappear. Thus, there should be two principal factors which determine whether a kin bias in food sharing is found: (1) the composition of foraging bands and (2) the optimum number of reciprocal food-sharing partners. The factors which affect the composition of foraging bands may be quite complex and unrelated to food sharing; these factors have yet to be isolated. The optimum number of food-sharing partners should be a function of the resource acquisition pattern, positively correlating with a predominance of large valuable packages which are sporadically and nonsynchronously acquired.

Damas's (1975) account of differences in the pattern of food sharing among Eskimo societies is of some interest here. The Netsilik Eskimo, who live in large extended families that pool food resources, have fewer seal-sharing partners than the Copper Eskimo, for whom isolated nuclear-family residence is the norm.

Cooperative acquisition. That game items almost exclusively acquired cooperatively are not shared more than those generally acquired by single individuals suggests that cooperative-acquisition reciprocity is not a necessary condition for the evolution of food sharing among predators. Nevertheless, it is possible that the reason we could find no difference in the sharing of cooperatively and solitarily hunted game is that all game is shared with the entire band.

There are data, however, which suggest that this is not the case. Some fruits consumed by the Ache are acquired cooperatively in that one individual climbs the tree and shakes the fruits down so that other band members may collect them. Our observations of such cases suggest that the "shakers" tend to receive fruits only from their spouses. In fact, some of the fruits acquired in this manner (e.g., *virella*) are shared least of all foods. Data on food sharing among social carnivores and primates also do not support the cooperative-acquisition hypothesis. While both social carnivores and meat-eating primates are reported to hunt cooperatively, many, if not most, instances of meat sharing do not involve cooperation among the consumers. Among lions and chimpanzees, for example, latecomers who were not involved in making the kill often obtain shares (Schaller 1972, Teleki 1973). All the data seem to indicate that the increased package size and nonsynchrony of acquisition associated with predation are the principal determinants of the more extensive food sharing found among predatory animals, including human foragers. It may be that cooperative acquisition is a consequence rather than a cause of food sharing.

Conservation. There was no empirical support for the hypothesis that foragers share resources to prevent overexploitation of resources. In fact, the complete absence of any practices obviously designed to check overharvesting of resources among the Ache suggests that widely held notions about resource conservation among hunter-gatherers (e.g., Hayden 1981) should be reconsidered. Evolutionary theory predicts that several conditions must be met for conservation strategies to be favored. Individuals must be able to exclude competitors from resource patches. The costs of that exclusion and of the conservation practices themselves must be outweighed by the advantages of maintaining a steady harvest in the protected patches (cf. Dyson-Hudson and Smith 1978). Since human foragers tend to take resources which are widely scattered (i.e., difficult to defend) and fairly unpredictable in their occurrence (i.e., not worth maintaining constant vigilance over), such conservation practices seem unlikely for most hunting and gathering groups. It would be interesting to determine whether the above conditions predict variation in the extent to which hunter-gatherers practice conservation.

There are some data suggesting that foragers do not share food to prevent the overexploitation of resources for other groups as well. Data on hunting among the !Kung Bushmen do not support the conservation hypothesis. The Dobe !Kung harvest only some .7% of the herbivore population in their area per year (Hill 1983). Data provided by the Utah Fish and Game Department indicate that 8–20% of the herbivore population (depending upon their reproductive rate) can be harvested without affecting population size. This implies that the !Kung would have to increase their harvest at least tenfold before being in danger of overexploiting their game resources. Yet, the !Kung share their meat resources extensively.

Tolerated theft. While the data suggest that Ache food sharing is not the outcome of contests over valuable food items, they do not imply that the threat of theft is not "felt" by Ache foragers. The decision to share may be affected by the consequences of not sharing (i.e., possible costly contests over food) as well as by the benefits associated with the increased nutritional status associated with reciprocity. In other words, an additional impetus to sharing might be that others would attempt to take the food forcibly if it were not shared and if the conditions of tolerated theft were met.

Reciprocity. In addition to finding that package size and synchrony of acquisition predicted variation in the sharing of different food resources, we also examined the extent to which individuals benefit from the reciprocal sharing of food. Given the assumption that the nutritional value of units of food energy diminishes with the amount available, we found that almost all individuals achieved higher nutritional status by sharing food. The data also showed that meat sharing generated the greatest increase in nutritional status, followed by the sharing of honey and then by that of other collected resources. This result is consistent with the fact that Ache foragers share meat most, followed by honey and then by other collected resources.

This increase in nutritional status was due to the pattern of resource acquisition exhibited by Ache foragers. Individuals frequently acquire large amounts of food (sometimes as much as 150,000 calories) on single days and little or none on other days. This is particularly true of meat resources, which make up the bulk of the Ache diet. Since the Ache do not store food, individuals experience a pattern of fluctuating abundance and scarcity. By sharing food, they substantially reduce day-to-day variation in individuals' consumption.

As mentioned above, however, there are features of the Ache food-sharing pattern which are not consistent with tit-for-tat reciprocity. There are consistent differences between individuals in foraging skill which do not appear to be reflected in differential food consumption. Thus, the form of food sharing practiced by Ache foragers appears to reflect a band-level pooling of resources rather than a strict tit-for-tat reciprocity.

One possible interpretation of these results is that group-rather than individual-level selection is responsible for food sharing in Ache bands. According to this interpretation, food sharing benefits the group as a whole and individuals sacrifice their own fitness interests for the good of the group. Food sharing might, for example, allow larger groups to assemble by supporting individuals who could not survive on their own and therefore afford a competitive advantage over other groups when conflict arises. The major problem with this interpretation is that group selection is highly unlikely, especially when learning is involved in the behavior in question. If an alternative strategy existed by which individuals could increase their own fitness at the expense of the group interest, some individual would eventually discover and experiment with it. Since, by definition, individuals who are more fit become more prevalent in the population over time, the group-selected strategy would eventually disappear. Moreover, since humans are so proficient at observing the behavior of others and imitating "successful" strategies, a "mutant" strategy which confers

higher individual fitness should quickly invade the population.¹²

A second possible interpretation of our results is that, for individual foragers, hunting success is so unpredictable that the band-level pooling of resources yields the highest overall nutritional payoff for all foragers, even though some benefit more than others. According to this interpretation, individuals who opted for a strict tit-for-tat reciprocity would be selected against because of the possibility of a long stretch of "bad luck." If the pattern of food sharing were such that an individual, having given a unit of food to another, would not give again until an equivalent unit had been returned, persons who did not acquire food for some time might experience severe nutritional stress. When resources are pooled at the level of the band, individuals who are undergoing a prolonged period of underproductivity will still be ensured food. Thus, even above-average foragers may be willing to give more than their share in order to avoid the risk of long stretches without food.

The problem with this interpretation is that it does not conform to the pattern of work effort exhibited by Ache foragers. If all food were pooled at the band level, above-average hunters would quit once they had acquired the mean amount acquired by others because they only benefit slightly from the additional food they would acquire from extra labor. In fact, the opposite is true. There is a positive correlation between the rate at which foragers acquire food and the number of hours they work (Hill and Hawkes 1983, Hill 1983, Hawkes, Hill, and O'Connell 1982). This suggests that there must be some payoff for acquiring more food than one consumes.

Given these findings, a likely explanation is that Ache food sharing is the result of two kinds of reciprocity: tit-for-tat and trade. According to this model, individuals benefit in different ways from food sharing. While all foragers reap the benefits of reduced day-to-day variation in food availability, low producers receive more food than they acquire whereas high producers gain other kinds of fitness benefits. Low producers accord some benefits to high producers in exchange for the extra food they provide. High producers, in turn, hunt more because providing others with food is the optimum strategy for maximizing their fitness. If this is true, it implies that, while from the perspective of nutritional status food value may diminish with quantity obtained, the *fitness* value of food may not diminish with quantity obtained because it can be exchanged for other fitness benefits. Figure 3 illustrates this point.

Why should low producers accord benefits to high producers, and how could these benefits translate into higher fitness? One important avenue through which high producers might receive preferential treatment is the threat of their leaving the band and joining another. The Ache do not appear to maintain a unilocal residence pattern, and considerable interband mobility seems to characterize both the past and the present. Other things being equal, an exceptionally high producer would presumably be a welcome addition to any band. Thus, high producers could expect better treatment than average or below-average producers to encourage them to remain in the band.

What kinds of better treatment might high producers receive? Preliminary review of unanalyzed demographic data suggests that infanticide is frequent and that decisions concerning whether particular children should be killed are sometimes made with the input of many band members. It is possible that

¹² It might be argued that members of the band would penalize individuals who chose strategies which maximized individual fitness at the expense of group interests. If, however, this "penalization" actually reduced individual fitness to the point where the alternative strategy which maximized group benefit was also the best individual strategy, there would be no conflict between individual- and group-level fitness.

the offspring of high producers are less likely to be killed. It is also possible that, when someone closely related to a high producer becomes ill, people may be more willing to remain in one location (at the expense of foraging returns) so that the sick individual may recuperate.

If such benefits accrue to the families of high producers, they should be amplified by sexual selection. High producers should be more attractive as mates (as should be their offspring, if foraging skill is inherited). The divorce rate among the Ache is extremely high; an individual may have more than fifteen spouses in his or her lifetime. The ability to choose when to keep a spouse or when to divorce in favor of another could confer higher fitness, especially since women appear to vary considerably in their reproductive potential over time. High producers might also experience increased access to extramarital sex in response to the threat of interband mobility. By copulating with high producers, females might encourage them to remain in the band because of the possibility that the offspring produced might be theirs. Low-producing males might also be more tolerant of adulterous relationships between high producers and their wives because the costs in terms of uncertainty of paternity (within limits) are outweighed by the benefits associated with more food for their children. For the same reasons, both the sons and daughters of high producers might be able to find better mates more quickly than do other young adults. If affinal ties tend to keep families together, one way of assuring a steady supply of food might be through marriage to the close kin of high producers. Preliminary analysis of demographic data supports these propositions. High-return hunters are reported to have more extramarital sexual relationships than poor hunters, and their children survive in significantly greater numbers (Kaplan and Hill 1985).

Other, less concrete benefits might be important as well. Men generally allow young boys and adolescents to accompany them while foraging, but they also appear to evidence marked preferences in this regard. If the hunting ability of the youth and of his father affect the likelihood of their accompanying skilled hunters and the quality of instruction they receive, then exceptionally skilled adolescents and the sons of high producers might obtain skills and friendships that other youths do not. Future field research on the Ache will focus on these questions.

The most general prediction generated by this research is that the temporal character of resource acquisition should determine both the amount and pattern of food sharing. Food sharing should occur when (1) individuals experience temporal

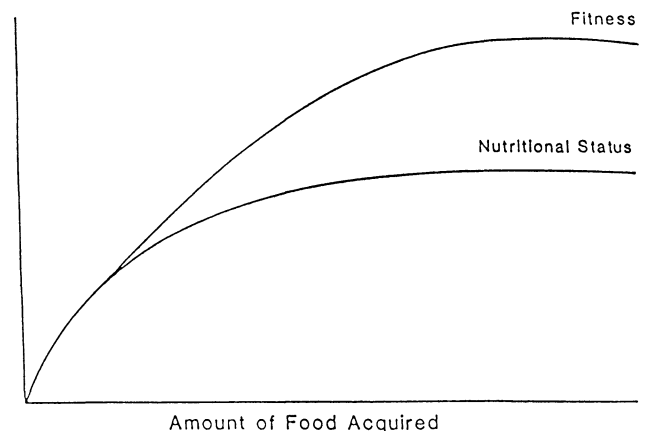


FIG. 3. Nutritional status and fitness in relation to amount of food acquired.

fluctuations in the amount of food they have available for consumption such that a point of diminishing returns in food value is sometimes reached and (2) the timing of these fluctuations varies across individuals. A resource should be shared to the degree to which its pattern of acquisition meets these conditions.¹³

These two conditions would most likely be met by the acquisition patterns of resources which yield high returns upon encounter but are relatively rare and unpredictable in their location. Game items are most likely to exhibit these qualities because they yield large quantities of calories, are mobile, and are relatively rare compared with grasses, leaves, and even fruits. Honey is also likely to meet these conditions because it often yields as many as 100,000 calories but is found only sporadically in somewhat unpredictable locations. Fruits and nuts often come in large quantities but are less rare and more predictable in their occurrence. Whether they are shared or not should depend upon whether most individuals in the band simultaneously come upon the resources. If not, sharing could result from temporal fluctuations in the calories they provide.

How do these predictions match data on food sharing in different social groups? Among nonhuman animals, the predictions tend to be supported by the data. As mentioned above, social carnivores are reported to share food among adults on a regular basis whereas no herbivores or folivores regularly share food. Primates are reported to share meat and large, rare fruits but not leaves and small fruits (Hamilton and Busse 1982, Hausfater 1976, Strum 1981, Tano 1981, Teleki 1973, Wrangham 1975).

While few quantitative data exist for human foragers, ethnographic reports suggest that the predictions are largely met for humans as well, though several problems remain unresolved. All human foragers take these large packages but vary in the extent to which their diet consists of high-return resources. The Shoshoni of western North America are reported to have eaten mostly seeds and nuts and not to have shared their food widely (Steward 1938). The Tiwi of Australia are reported to consume mostly foods collected by women and to share little (Hart and Pilling 1960). The !Kung, who eat large quantities of both meat and nuts, share their meat resources widely and mongongo nuts much less (Lee 1979, Marshall 1961). Both the Onge of the Andaman Islands (Bose 1962) and the Hill Pandarum of India (Morris 1982) share meat and honey widely but not collected vegetable resources. Almost all Eskimo groups (with the exception of the Nunamiut [Binford 1978]) share meat widely both at the community level and with reciprocal seal-sharing partners (Damas 1975). For these groups meat comprises more than 90% of the diet.

A great deal of work remains to be done, however, both in terms of testing the generality of these principles with other organisms and human groups and in terms of specifying how features of the resource distribution pattern interact with food sharing. For a more comprehensive model of reciprocity and food sharing, the predictions outlined above are not sufficiently specific. For example, how large, in relation to the body size of the organism in question, must the package be in order for sharing to evolve? Throughout the animal kingdom, there is a continuum of variation with respect to the package size and environmental distribution of the resources exploited. Food sharing is perhaps more profitably viewed as a continuum as well. At one extreme is complete intolerance to the presence of others when feeding. At the other is full-blown exchange of foodstuffs. Between these two extremes are passive tolerance of simultaneous feeding and active food calling to recruit conspecifics to resource patches (such as a large fruiting tree). Modeling and testing the relationship between features of re-

source exploitation and the sociality of feeding should continue to be an interesting and demanding enterprise.

In addition to the character of resource acquisition, the potential for food storage should affect variation in the extent to which different social groups share their resources. If food is stored, temporal fluctuations in resource acquisition do not necessarily entail temporal fluctuations in *food availability*. This implies that a point of diminishing returns may not be reached even when large quantities of food are obtained because units of food may be saved for times when little or no food is acquired.

The case of the Eskimo raises some interesting questions about the effects of food storability on sharing. In keeping with the predictions of both the tolerated-theft and tit-for-tat-reciprocity models, the Nunamiut are reported to share meat in the summer, when it is not stored, but not to do so in the winter, when they are living off caribou stores acquired in the fall. The Iglulik, Copper, and Tlingit Eskimo, however, share their food even though there is no apparent reason they could not store food and keep it for themselves without sharing (Damas 1975). There is one major difference between the Nunamiut and these other three groups. For the Nunamiut, the fall caribou hunt represents the last major opportunity for hunting until the following spring; the caribou migrate in large herds and may be killed in significant numbers for a short period during the fall and then move out of their range. In contrast, these other three groups hunt seal throughout the winter, and there is no single seasonal glut. This suggests that the storability of food is not the only factor in determining whether large packages will be shared and consumed when they are captured or stored and consumed by the family of the acquirer. There are probably opportunity costs associated with storage which favor food sharing when food is more regular in its seasonal distribution (Blurton Jones n.d.).

If theft of food stores is a real threat, then storage represents an important opportunity cost because stores will have to be guarded. In the case of the Nunamiut, this cost is small because opportunities for continued foraging are low. In the case of these three sealing groups, guarding food stores entails sacrificing foraging time which could be used to acquire more meat. If this is correct, it suggests that reciprocity could be favored primarily against a backdrop of potential theft.

It is also possible that storage involves some more straightforward opportunity costs such as decreased mobility. Copper Eskimos are reported to move their camps in relation to the locations of seals (Damas 1972). If the existence of food stores renders mobility more difficult, there could be net benefits to reciprocal food sharing even though meat could be stored. Similar arguments could be made in explaining why the !Kung do not store meat for long periods (cf. Lee 1979:156). The question of what costs are entailed by food storage and what factors condition variation in its occurrence deserves further investigation.

There are several other conditions that could affect variation in food sharing. One is the existence of an economy of scale in resource acquisition (cf. Blurton Jones n.d.). If some resources can be acquired more efficiently when taken in large quantities, reciprocal labor and food sharing could be selectively favored. In the case of female gathering, which is competitive with child care, all individual women could conceivably benefit from turn-taking in food acquisition and child care if either or both gathering and child care were characterized by an economy of scale. If the costs of child care per child decrease with the number of children being cared for and/or the resources collected are acquired at a higher rate when they are taken in large quantities, then females should either take turns in these two activities or specialize and share food. This may be the case with the Ache and is currently being studied by Ana Hurtado. This may also explain why lions and elephants are reported to nurse and care for each other's offspring (Doug-

¹³ The ability to transport food should greatly enhance the effects of these two conditions on food sharing.

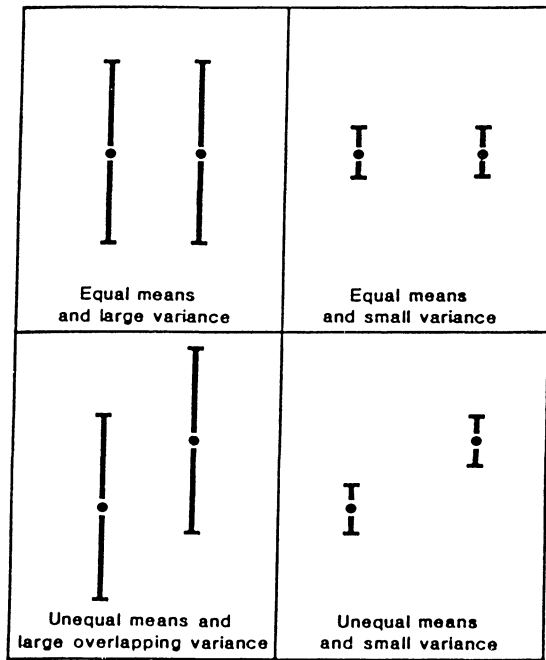


FIG. 4. Dyadic model of four possible resource acquisition patterns.

las-Hamilton and Douglas-Hamilton 1975, Schaller 1972). The factors which affect whether an economy of scale exists and whether those factors predict cooperation and food sharing have not yet been investigated.

Another possible condition which could affect the occurrence of reciprocity could be nonsynchronized temporal variation in the costs associated with resource acquisition. When a female is caring for a newborn baby, the cost of foraging may be greater than when the offspring is more mature. Thus, females might establish reciprocal relations over long periods of time such that they acquire and share more food when their offspring are mature and less when they are young. Ache women who are currently nursing infants produce significantly less food than other adult women, even though they do not eat less (Hurtado et al. n.d.). Although these results are suggestive, more data are necessary in order to determine whether such long-term reciprocity is actually occurring.

Figure 4 illustrates four possible ecological conditions that should affect the appearance of tit-for-tat reciprocity and trade. It represents simple dyadic relationships between individuals in their acquisition of some valuable resource such as food. The midpoint of each line represents the mean amount acquired, and the end points represent the variance. Where variance is low and means are approximately equal (*top right*), neither reciprocity nor trade will occur because neither confers fitness benefits. Where variance is high but means are equal (*top left*), we expect tit-for-tat reciprocity but no trade. Tit-for-tat reciprocity should reduce daily variance in the amount of the resource available. If there is a point of diminishing returns associated with this resource on a daily basis but not over longer periods of time, tit-for-tat reciprocity should increase fitness. Where variance is low and means are substantially different (*bottom right*), tit-for-tat reciprocity is not expected because it should not confer fitness benefits. Trade, however, may occur if there are other resources (such as status) which are (1) more valuable to the high producer than some fraction of the resource he/she has in abundance and (2) less valuable to the low producer than extra units of the resource of which he/she has little. Where variance is high and means are different (*bottom left*), both tit-for-tat reciprocity and trade may occur. The predictions of this model can be tested by comparing dif-

ferent social groups whose ecology and resource acquisition patterns are different and by comparing different resources within the same society.

CONCLUSIONS

With a specific focus on food sharing and the factors that predict its occurrence, we have explored two issues in this paper: (1) the extent to which models derived from evolutionary ecology and research on nonhuman organisms can provide productive hypotheses and research strategies for understanding variation in human social behavior and (2) the extent to which research on human social groups can contribute to general and uniformitarian theories of organismic behavior and its evolution. These issues are not themselves matters for empirical test. However, it does appear that the application of evolutionary ecology to the study of human food sharing, at the very least, generates a coherent set of research questions for which definitive answers may be obtained. It also appears that the answers obtained from the study of food sharing among Ache foragers are largely consistent with empirical generalizations derived from the study of other animal taxa and should be useful for more general theory building on the evolution of food sharing.

Comments

by ROWE V. CADELIÑA

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Kaplan and Hill's article seems to me to dehumanize the human transactors in the process of food sharing. This is not surprising in a paper that tries to test hypotheses drawn from the behavior of lower forms of animals using human beings.

On tolerated theft, the writers claim that "when some individuals acquire large amounts of resources while others acquire none or little, the tolerated-theft hypothesis predicts that possessors will permit nonpossessors to 'steal' from them because the cost of defense to the possessor is greater than the value of retaining the 'stolen' portion." This claim does not stand up to close examination. It is common in developing countries, and I suppose in developed countries as well, for "stealing" to be viewed differently depending on the status of the thief. Poor individuals who take things from others (especially from the rich) are generally accused of or prosecuted for stealing. In contrast, when a wealthy individual takes something, especially from the poor, he is seldom prosecuted but rather praised for being a "down-to-earth" fellow who appreciates the things of the poor. This is how the social system works.

Kaplan and Hill conclude that the conservation hypothesis is not supported by their Ache data. Conservation may, however, be either an antecedent to food sharing or a consequence of it. In the first instance, the transactors are usually aware that they are practicing conservation; in the second they are not. These two instances have to be carefully differentiated in the analysis. Kaplan and Hill's article deals with situations in which conservation may take place as a result of food sharing. In such situations, people are generally unaware that it is happening.

In their conclusion, Kaplan and Hill note that the answers obtained from the study of food sharing among the Ache foragers are largely consistent with empirical generalizations derived from the study of other animal taxa. They believe that these are useful for more general theory building on the evolu-

tion of food sharing. This statement shows their tendency to stretch the applicability of their generalizations derived from the lower forms of animals to human beings. Table 10 shows that most of the hypotheses tested were not supported by the Ache data. This suggests the difficulty and perhaps the inappropriateness of using empirical generalizations derived from the study of other animal taxa to explain the complex human behavior of food sharing.

by BRIAN HAYDEN

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Kaplan and Hill's topic is important, and they approach it with uncommon lucidity. I can think of no better treatment in an article of this length. My only quibble is with their dismissal of evidence showing that most hunter/gatherers display evidence of conservation behavior, as documented in Hayden (1981). While conservation behavior is certainly not universal among hunter/gatherers, it is at least common. To explain this variation would require an analysis similar to Kaplan and Hill's article. I am also surprised that they single out this rather minor point of my article without acknowledging the suggestion there that food sharing exists because of its reciprocal advantages. Their delineation of alternative hypotheses and their implications is, however, exemplary; there are few finer pieces of analysis in the anthropological literature. Congratulations are in order.

by DAVID CHARLES HYNDMAN

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Kin selection, tolerated theft, reciprocity, and cooperative acquisition, the cost/benefit models sociobiologists use to account for food sharing among nonhuman animals, are applied by Kaplan and Hill to explain the presence and extent of food sharing among adult Ache foragers in terms of the maximisation of inclusive fitness. Not until a quarter of the way through their paper do the authors acknowledge that there is controversy with regard to sociological vs. sociobiological explanations of food sharing among humans. Their evasion of the debate on the grounds that it is beyond the scope of their discussion is asymmetrical considering the lengthy attention given to nonhuman food sharing. Given that the focus is on adult food sharing, there is altogether too much discussion of kin selection, which overwhelmingly involves the occurrence of food sharing between parents and offspring. The authors' position is that reciprocity (meaning reciprocal altruism) and kinship are closely connected in human societies because partners in reciprocal altruism are often classed as kin. Combining the perspective of individual fitness with the view that the young of human conspecifics particularly benefit from provisioning because they are altricial rather than precocial radically alters the conventional anthropological position that food sharing among foragers is characterised by a notion of reciprocity as summarised by Harris (1980:228) and cited here.

The hallmark of anthropology is contextual analysis, the recognition that different aspects of a culture are interrelated. Contextual analysis goes beyond the mere cataloging of events to attempt to understand human behaviour. The contextual analysis provided in the empirical-tests section is insufficient for the authors to argue plausibly for a radical new interpretation of food sharing and reciprocity based on sociobiological models. "Consumption events" alone are an inadequate data set to measure the applicability of different fitness currencies to the understanding of food sharing.

The authors make the ethnographically unsubstantiated claim that nine foraging trips can be equated with nine forag-

ing bands, each engaging in band-level sharing. Ache foragers are now settled mission communities of hunter-horticulturalists, and even if we accept the assertion that mission relationships do not affect sharing in the jungle, there is no contextual social organisation evidence indicating that these foraging trips equate with discrete foraging bands. Cross-culturally the personnel of forager camps and subsistence trips are known to fluctuate, and their food sharing is known to be enveloped in wider networks of kin. An analysis based on consumption events is vulnerable to the decade-old critique of caloric reductionism (Brookfield 1972, Cook 1973, Vayda and McCay 1975). Moreover, the relationship of fitness currencies to food sharing is measured only in terms of calories consumed; no allowance is made for calories expended in subsistence behaviour. Why should weight or calories be a better predictor of sharing than expenditure? Given researcher-to-forager ratios of 1:2.2-1:3.2, one would think that acquisition information would also have been collected. In fact, the authors allude to having collected this information but make no systematic effort to demonstrate the predictive value of calories acquired per hour foraged or of the number of hours worked. It is therefore surprising that they conclude that the temporal character of resource acquisition should determine both the amount and the pattern of food sharing.

Their not embedding their analysis contextually in Ache culture results in other interesting misinterpretations. Single men are designated as the clear "losers" when food is pooled on foraging trips. The authors' interpretation would be well informed by Siskind's (1973) work with the Sharanahua hunters of the Peruvian rain forest. Instead of suggesting that foraging skill may be inherited, they should concentrate on the prestige and political power that come to successful unmarried hunters and give more attention to the inclusive-fitness potential of hunters' extramarital affairs. Elsewhere the authors use Harris's definition of reciprocity to generate a conservation hypothesis. When they observe the Ache destroying beehives, chopping down fruiting trees, and killing and eating bush dogs they label them as anticonservationist. There is no such thing as an objectively ascertained or culture-free designation of an endangered species. Accepting that *Speothos venaticus* is declared an endangered species by the WWO simply points out that the authors fail to appreciate that resources of the Ache, like those of other indigenous peoples, are rapidly being caught up in the conflicting forces of conservationists who want to conserve them and the ancestral owners who want to use them. While the Ache may not live in Rousseauian harmony with nature, their practices of environmental manipulation probably provide a sustained resource yield over time.

by RICHARD J. PRESTON

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The use of cost/benefit analysis to construct statements of a universal algebra of animal behavior is as much an indicator of reliance upon the dubious conceptual metaphors of late positivism as it is a heuristic for generalizing about behavioral evolution. Like the Law of Parsimony, cost/benefit analysis would be adequate theoretically only if the world actually were constructed according to these principles of organization and selection—a condition so remarkable that it would have to be attributed to God, no matter how well the correlations turned out in the particularities of abstracted empiricism. Probably this accusation of tacit teleology will draw some reproach regarding levels of argument, but the point is not trivial. Why is there such reliance on labels for behavior types that need to be set in quotation marks? Where are the more confident concepts grounded in the specific behavioral environments from which the data are abstracted? This is particularly striking with the Ache data, where extensive quantitative detail remains unac-

accompanied by ethnographic insight. Yet the Ache will somehow serve as a metaphor for human foragers generally, showing that proximity goes with sharing, supporting cooperation, and that success in the hunt correlates with success in mating. Where is the interplay of the egalitarian ethic and the achievement of esteem so common in hunter-gatherers? These ethnographic concepts, having a moral rather than a natural basis, are excluded from inquiry. The opportunity costs are too great, because the phenomena are so rich. Pity.

by ERIC ALDEN SMITH

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Theory from evolutionary ecology has shown great explanatory power in studies of other species, and preliminary applications to humans exhibit great promise (review in Smith 1983). Furthermore, the explanation of variation in patterns of human food sharing (or resource sharing in general) is a task most anthropologists would consider important—more important than the more limited topics, such as prey choice and diet breadth, heretofore the centerpiece of evolutionary ecological research on humans. Hence, I am very sympathetic with the general goal of this essay. Furthermore, I applaud the authors' effort not only to present and apply theory but to discuss alternative models and predictions and test them (as well as their data allow) in a rigorous fashion. Although tedious to many readers, such careful juxtaposition of data and theory is evidence of a much more mature approach to inquiry than the plausibility arguments and literary persuasions that dominate most areas of sociocultural anthropology today.

It is my opinion that the authors accurately portray theory and research pertinent to food sharing conducted by biologists. The coverage of related work by anthropologists is much spottier, and the contrasts made between the ecological arguments and the anthropological ones, while neat and telling at some points, are superficial at others. But I leave a defense of traditional anthropological approaches to food sharing to practitioners of the same.

Despite my overall enthusiasm, I do have some criticisms, quibbles, and additions to make. First, I am not at all clear about the purposes served by reviewing the data on food sharing in nonhumans. These data demonstrate the wide variation in such behavior found between and within other species and serve as independent tests of theory, but I fail to understand how they can be employed to explain human patterns. My objection is not based on a view of humans as incomparable to other species or outside the purview of Darwinian logic; while I am convinced by certain arguments that cultural inheritance makes a difference, I am also convinced that culture is subject to natural selection and coevolves or interacts closely with genetically transmitted instructions (Boyd and Richerson n.d., Durham n.d.). Instead, my objection to citing studies of carnivore or chimpanzee or bee-eater societies is that at best these studies play a heuristic role for anthropologists, while at worst they may be misinterpreted as another attempt to argue, à la Konrad Lorenz, that "if wolves and baboons do it this way, then humans must too." Contrary to Kaplan and Hill's assertion that "expectations" about food sharing are "suggested by the data on nonhuman animals," I would argue that data do not predict or explain, theory does. Unless the proximate behavioral mechanisms are believed to be the same and we are postulating strict evolutionary homology, we should view data from other species as strictly heuristic, not explanatory.

The discussion of the relative explanatory power of "package size" versus variance in daily harvest in accounting for food sharing is intriguing. It would seem from a strict interpretation of the tit-for-tat diminishing-returns model that only the latter is strictly relevant and package size should not make an *independent* contribution to explaining sharing—yet the data

suggest it does. In fact, package size has been reported as a strong influence on sharing in quite a number of hunter-gatherer societies (Smith 1981:46). It may be that this incongruence between theory and data is resolved if we consider the costs of making decisions: a simple cultural convention concerning sharing large packages might not exactly match predictions from a diminishing-returns curve, but it would simplify decision making and reduce opportunity for disputes. I leave it to the authors to consider the relevance of this hypothesis to the Ache.

There are a few semantic slips in the article. First, the reference to trade as marked by the exchange of "different fitness currencies" is puzzling; do the authors mean different *proximate* currencies (correlates of fitness)? Surely they cannot mean different measures of fitness (e.g., inclusive, individual, mean population). Second, the claim that "individuals who are more fit become more prevalent in the population over time" garbles a couple of elements of neo-Darwinian logic. It would make much more sense to say that *traits* (or their underlying instructions, whether "genes" or "memes") that are more fit replicate at a faster rate than competing traits and thus become *relatively* (not necessarily absolutely) more abundant in future generations (see Dawkins 1982: chap. 10 for an extended discussion of the muddles generated by loose talk about "fitness"). Finally, it is presumptuous (or myopic) of Kaplan and Hill to claim that the prediction of sharing under specific spatiotemporal patterns of resource acquisition is "generated" by their own research. Rather, it is supported—and supported with admirable clarity and effort—by this research but has been independently derived by several other biologists and anthropologists (Schaffer 1978, Harpending 1981, Smith 1981). Of these, Schaffer's is the most general and rigorous formulation, but Harpending should be consulted for his ingenious formal argument that there will be little kin-preferential sharing in the case of resources with high "fitness saturation" (i.e., rapidly diminishing marginal fitness effects). That means that the pattern observed among the Ache, where perishable or immediately consumable resources such as meat and honey are shared with little or no regard to kin ties, is in fact predictable from first principles of evolutionary ecology. The converse prediction of high degrees of kin preference in transfer of resources with low saturation (e.g., long-lived resources such as arable land) is also generated by Harpending's model, and the obvious place to test it among the Ache is back at the mission settlement.

In sum, this paper is an excellent, even state-of-the-art, demonstration of the anthropological utility of theory from evolutionary ecology. Since the state of the art is far from perfect, and since it is difficult to master the substance of one discipline, let alone two simultaneously, the paper has flaws. These are minor compared to the overall accomplishments, however. The strongest contribution of this paper is found in the wedding of carefully collected data to tests of alternative hypotheses (e.g., tit-for-tat vs. tolerated theft). The Ache data on food sharing are particularly valuable because of their high quality: excellent sampling methods, carefully quantified, and a wide range of variables. The contributions to theory are less original; however, the model sketched in figure 4 is stimulating and should reward future tests.

by DAVID E. STUART

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Kaplan and Hill's paper is well organized and thoughtful, makes good use of field data from Paraguay's Ache foragers, and effectively points out that food sharing among hunter-

gatherers is a topic anthropology must master before fully pursuing comparative models of evolutionary change.

The paper's major findings are consistent with patterns found among the Ona and Yahgan of Tierra del Fuego. Ona men, terrestrial guanaco hunters, often carried kills great distances to share with their foraging party. In some seasons, seals were also hunted and shared. But small fish, eels, and grass seeds, primarily gotten by women, were shared at the nuclear-family level or not at all. Among the canoe-going Yahgan of Beagle Channel, seals were shared when canoe travel was possible, but daily mussel collecting was often an individual pursuit even among children.

Unfortunately, the authors do not really press the evolutionary implications of these sharing patterns. Anthropology has yet to explain why, in the course of cultural evolution, some societies were transformed into sedentary horticulturalists while others remained foragers, even in similar ecological circumstances. If one looks more closely at the Ona, several tentative clues emerge.

Even after European immigration had pressed Ona society into half its precontact territory, successful hunters often took several wives. In 1900, one Houshken in the Hyewhin Lake district had 11 wives. Much of the year his band was a "nuclear family," large as it was, so "bandwide sharing" directly benefited him through his offspring. As territorial pressures increased, his two brothers (also skilled hunters with several wives) joined him, obsessively hunting guanaco. This both increased his prestige and protected his hold on the Hyewhin Lake district—a stunningly effective "scorched-earth" policy. He also had ample female foraging labor to fall back on when his district became overhunted.

In striking contrast, the eccentric Talimeot lived near the Atlantic coast with his wife and son. Almost exclusively a cormorant hunter, he seldom traveled with any foraging group, had a semipermanent home camp, was largely self-sufficient, and, though he regularly offered cormorant to hungry visitors, was little involved in reciprocal sharing. Other Ona hunters, considered lazy or incompetent, were derided as "having to live by the sea and be fed fish by their wives." Clearly, some were simple outcasts from the foraging parties in which food sharing was so important.

These examples are pertinent because they indicate that the Ona, a "classic" hunter-gatherer society, may be economically more heterogeneous and less egalitarian than generally supposed. Therefore, it is critical to know who is *not* regularly invited to participate in foraging parties and *why*.

I hope that Kaplan and Hill eventually have the opportunity to find out who, if anyone, gets left behind when Ache foraging parties are formed and who, if anyone, is eccentric enough to "tough it out alone." If fieldworkers also focus on situations in which large-package food-sharing is interrupted, refused, or withheld, we may be better able to discuss the evolutionary consequences of food-sharing patterns.

by DAVID R. YESNER

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This rigorous analysis of food-sharing practices represents an additional well-reasoned contribution from the Utah school of evolutionary ecology (also represented by Kristen Hawkes and Jim O'Connell). Kaplan and Hill's views of human adaptation, while cast in a more frankly genetic mold than other analyses of "optimizing behavior" in foraging societies, stop far short of more dogmatic approaches to sociobiology. This is demonstrated by their willingness to adopt the method of multiple working hypotheses and to discuss problems in designing and operationalizing field tests of those hypotheses.

Five major explanations are presented for the existence and extent of human food sharing (although nowhere are these

considered mutually exclusive). Some of these models assume that mutual benefit occurs as individuals attempt to maximize their inclusive fitness in direct interpersonal relations, either through time-delayed exchanges of food energy ("tit-for-tat" reciprocity), trading energy for increased fertility (preferential treatment of kin, sexual rewards for food), or trading energy for decreased mortality (tolerated theft, decreased infanticide, increased medical attention). Other models assume that fitness maximization occurs more indirectly, either through rewarding group participation in foraging (cooperative acquisition) or through limiting overexploitation of resources (conservation). (The latter is a problem only insofar as there are differential abilities for resource harvesting so that individuals with greater abilities are forced to share in order to maintain their own future yields.)

The Ache data clearly serve as a good base to test (and reject) at least some of these hypotheses. As a genetically based argument, kin selection appears to be applicable only at the parent-offspring level; it is admitted that "social" kinship may be as powerful as "biological" kinship as an organizing principle for food sharing. Some of the difficulties of operationalizing tests of human kin selection (e.g., evaluating differences in reproductive potential) are outlined, and I would add to these differences in survivorship (average life expectancies). Although tolerated theft is initially offered as a powerful hypothesis ("If tolerated theft can account for the presence of food sharing . . . reciprocity need not be involved") it apparently will not work as a general explanation of food sharing because too much is given up. Cooperative acquisition fails as a hypothesis because cooperatively harvested resources are not more widely shared than other resources. (Cooperative acquisition is therefore seen as a consequence rather than a cause of sharing strategies.) The two remaining hypotheses (resource conservation and reciprocity) are less yielding to facile analysis. Resource conservation is rejected, but several questions need to be answered before it can be properly evaluated:

1. The Ache may eat endangered species, but are these only recently endangered species and not endangered by the Ache?

2. The Ache may not obtain more than 10% of their animal food from the mission, but do species have longer periods to regenerate now that the Ache spend less than half their time foraging?

3. For large, fatty game such as peccaries, could not an explanation for their intensive exploitation lie in the nutritional demands created by a protein- and fat-poor mission diet with a very low meat content?

4. It is true that, on the average, 6–10% of ungulate populations may be cropped for maximum sustained yield (depending on population age structure/sex ratio, ages/sexes harvested, etc.). Conditions are not always average, however—why couldn't the Ache be adjusting their yields to minimum animal population levels, for example?

5. It is argued that, since groups such as the !Kung harvest annually only 0.7% of their herbivore prey, they are in no danger of overexploiting their animal resources and thus have no need to practice conservation. In fact, however, couldn't this reduced harvest be the result of food-sharing practices which help to prevent overexploitation of resources?

This issue of causes and consequences lies at the heart of the debate over Harris's attempts to relate food sharing to conservation practices. It is essentially an epistemological question that will not readily yield to resolution. At present, it makes little sense to abandon resource conservation as one element of reciprocal food sharing.

Clearly, however, group-level reciprocity has additional functions, including increasing the nutritional well-being of the band. Why, then, can't group selection adequately explain the origins of this phenomenon? The authors reject such an explanation on the basis of the notion that selfish behavior will always spread in a population (i.e., be of selective advantage)

unless penalized—at which point, of course, inclusive fitness would once again come into play. Again, this is an epistemological issue. Nowhere is the principle of inclusive fitness actually tested; all hypotheses flow from this unifying assumption. Whether all behavior can be so reduced remains a matter for experimentation and debate, but this article shows that its consequences can be tested with data from extant foraging societies.

Reply

by HILLARD KAPLAN and KIM HILL
Salt Lake City, Utah, U.S.A. 22 XI 84

We will begin with some remarks about our general theoretical approach. Several of the commentators object to our frankly reductionistic approach to the problem of explaining variation in the extent to which organisms share food. Cadelina feels that we have “dehumanized” the human transactors in the process of food sharing. Hyndman argues that our approach suffers from a lack of contextual analysis that weakens our conclusions and leads to misinterpretations of the data. Preston remarks that, in our work, extensive quantitative detail is unaccompanied by ethnographic insight and, as a result, we sacrifice the richness of the phenomena under investigation.

Cadelina illustrates his point with the example of tolerated theft. He argues that we fail to recognize that humans differentially evaluate the taking of things from others in relation to their relative social positions. He feels that given these varying responses to expropriation, the tolerated-theft hypothesis is clearly inappropriate for human groups. The problem with this argument is that the existence of various social evaluations of “theft” is irrelevant to the empirical question of whether the predictions of the tolerated-theft hypothesis are met by human groups. That hypothesis simply predicts that, under the conditions specified in the test above, individuals will succeed in taking food from others because the value of the “stolen” portion of the possessor is less than the cost of defending it. It attempts to establish a relationship between general conditions and behavioral outcomes. If data acquired from different organisms, including humans, all tend to confirm the hypothesis, then we accept it as generally valid until it can be shown that some other hypothesis better explains the data. The existence of legal systems and specialized law enforcement bodies in state societies, as well as other forms of social response to theft in all human societies, complicates matters because it alters the costs and benefits of taking and protecting resources. It should not, however, a priori invalidate the hypothesis.

The phrasing of the tolerated-theft hypothesis may be a source of confusion. Terms such as “theft” and “stealing,” which imply specific social evaluations, should be avoided and replaced by less value-laden ones such as “taking” and, perhaps, “expropriating.” The use of quotation marks to which Preston objects was our attempt to remove the value labels from these terms. Quotation marks were not, however, employed to introduce vagueness into the operationalization of concepts. On the contrary, our goal was to be as rigorous as possible in the definition and reassessment of the concepts.

Hyndman is bothered that we have forsaken the “hallmark of anthropology,” “contextual analysis.” He feels that we have not recognized that “different aspects of a culture are interrelated” and states that “consumption events” alone are an insufficient data set for testing alternative explanatory hypotheses regarding food sharing. He does not, however, say *why* these are insufficient. We agree with Hyndman that many aspects of behavior are often interrelated but have purposely tried to find the smallest number of relevant variables that can account for most of the variation in patterns of human food sharing. We begin with few independent variables because

there is no need to build highly complex models if simple ones can be shown to predict the variance of interest. Whether or not such simple models can account for differences in sharing patterns across human groups becomes an empirical question. Our data suggest that perhaps they can. In simple terms, this means that although many different aspects of culture *may* be interrelated, the data suggest that many aspects of culture are *probably* irrelevant to the variance in certain cultural behaviors.

Hyndman also argues that nine foraging trips cannot be equated with nine distinct foraging bands. This is probably true, although initial review of precontact band compositions suggests that the foraging parties we observed are quite similar in composition to precontact bands. Again, however, it is important to emphasize that our attempt in this paper was to determine whether there exists a general empirical relationship between specific ecological conditions and behavioral outcomes and whether this relationship is explainable in theoretically coherent terms. We do not argue that the food-sharing pattern observed is due to the similarity of modern foraging trips to precontact bands. Given our findings and those of other studies reviewed above, it seems that a general relationship does exist between ecological variables and food sharing. If not, the fact that large, nonstorable, sporadically acquired packages are widely shared among primates, social carnivores, and humans is a remarkable coincidence.

This point is also germane to Preston’s critique. He seems to argue that regardless of the results of empirical tests, cost/benefit analyses could not possibly explain behavioral organization because if the world were that predictable it would have to have been created by God. We are not sure what Preston means by “the dubious conceptual metaphors of late positivism,” but if he means that we accept the assumption that the world is explainable *and*, to a large extent, predictable, we do not deny his charge. However, the existence of order in nature is not so miraculous to us. Many highly complex but ordered phenomena, such as radioactive decay, the production of enzymes through specific sequences of DNA, and the operation and construction of the vertebrate eye, have proven tractable to scientific inquiry without recourse to explanations in terms of divine intervention.

If one accepts the assumption that human behavior is explainable and predictable, another important epistemological question is by what methods adequate explanations will be most readily achieved. We accept the proposition that verifiable explanations require reduction of complexity. We do not see how “ethnographic insight” into the culture whole can lead to a cumulative understanding of human behavior. “Ethnographic insight” is frequently a code word for “subjective impression,” “personal interpretation,” or “poetic description.” Although we have a good deal of information on, and personal interest in, the particulars of the Ache sharing pattern and most other aspects of Ache life, we feel that the testing of hypotheses with general applicability is a more productive contribution to the study of man than would be a descriptive ethnographic account of “how the Ache do it,” no matter how “insightful.”

Several commentators (e.g., Cadelina, Hyndman, Smith) also object to our use of data and models from nonhuman animal research. Our treatment of animal behavioral ecology and of anthropological approaches to food sharing is admittedly unbalanced. There are several reasons for this. First, since the literature on resource sharing and cooperation in animals is vast and growing at an explosive rate, we reasoned that a summary review of the body of data and theory would be of some use to anthropologists, who are generally more familiar with the work done on human groups. Second, as stated above, we feel that the uniformitarian and positivistic ap-

proach employed by behavioral ecologists is likely to be more productive in explaining variation in food-sharing practices than particularistic ethnographic approaches. Third, and perhaps more important, we hope that a reciprocal exchange of data and theory will develop between anthropologists and nonhuman animal ecologists. We disagree with Smith that theory alone generates predictive hypotheses. We feel that there is a constant interplay between theory development, empirical tests, and further development of theory. We believe that anthropologists should make use of all available relevant theory and data in determining which hypotheses to test and what kind of data to collect. From our perspective, anthropology is a subdiscipline of biology, and the goal of anthropologists is not only to understand human behavioral variability but also to contribute to a larger understanding of organismic behavior in general. We are not suggesting, as Smith says, that "if wolves and baboons do it this way, humans must too." In fact, one of the lessons to be derived from modern ecological research is that organisms that are closely related phylogenetically can exhibit markedly different behavioral patterns while those that are quite phylogenetically distant can come to adopt very similar kinds of behavior. In explaining these patterns of convergence and divergence, the examination of feeding strategies has provided a great deal of insight and predictive power (e.g., Clutton-Brock and Harvey 1978, Wittenberger and Tilson 1981). We hope that our paper will stimulate similar studies encompassing a wide variety of organisms.

We will now respond to more specific comments in a more piecemeal fashion. Hyndman states that we fail to consider the predictive value of return rates and hours worked.¹ We are not sure to what kind of test Hyndman is referring (predictive value with respect to what?). However, if he is suggesting that we test whether foragers who produce more calories per hour foraged or who work more receive more food than others, the answer is clear. We report here that total calories produced per day does not correlate with calories of food consumed. Other papers published by the Utah Human Behavioral Ecology Research Group (e.g., Hill and Hawkes 1983, Hill 1983) show that number of hours spent hunting is positively correlated with calories produced per hour foraged. This implies that total calories produced is strongly correlated with both hours worked and return rates per hour and that they do not predict the distribution of shared food.

Hyndman's additional criticism that we misinterpret our results because we fail to recognize that sharing of excess food may produce other fitness benefits is difficult to understand. We explicitly state in the discussion section that we expect exceptional hunters to have increased social status. Moreover, our data show that high producers have significantly more extramarital sexual relationships than poor hunters and that they have higher overall reproductive success (Kaplan and Hill 1985).

Smith points out that the independent contribution of package size in predicting which resources are shared most may be explainable as a convenient cultural convention. Relative differences in package size are probably more easily discernible than is mean variance between families in the amount acquired of different resources. Therefore, if package size is a reasonably accurate index of average daily variance (and our data show that it is), it may be a more desirable measure to use when determining which foods should be shared most. We consider this to be highly likely but would also like to add that our measure of daily variance between families does not precisely correspond to the construct we hoped to test. It may be that people are less concerned with average variance between

¹Ethnographer-to-forager ratios cited by Hyndman are incorrect. He appears to have calculated the ratio of "ethnographers" to "Ache nuclear families" on foraging trips.

families of any given resource than the contribution of that resource to the *overall* variance between families in the total amount of food they have to eat. Moreover, because of differences in nutrients between food resources, some resources may be regarded as essentially equivalent calorie for calorie while others may not (Hill et al. n.d.). For example, mammalian meat resources may be essentially interchangeable whereas 1,000 kcal. of palm fiber may be valued less than an equivalent amount of meat. These possibilities complicate matters considerably, especially when differences in package size also correlate with nutritional differences (meat is generally found in larger packages than fruits, for example). We intentionally avoided the treatment of these complexities but hope that they will be addressed in future research.

We agree with Smith that the description of trade as marked by exchange of "different fitness currencies" is confusing. "Proximate currencies" or "correlates of fitness" is what we meant. Smith is also correct in pointing out that "individuals who are more fit become more prevalent in the population over time" is sloppily phrased; his restatement of neo-Darwinian logic is more accurate. Finally, we also agree with Smith, as should be clear from our introductory review of the literature, that the predictions we tested were not generated by our research but derived from the suggestions of others. In this regard, we apologize to Hayden for not citing his work when discussing the possible importance of reciprocity in food sharing.

Yesner and Cadeliña make several interesting points about our rejection of the resource-conservation hypothesis. We agree with Cadeliña that it is important to distinguish between the hypothesis that food sharing is practiced by human hunter-gatherers as an attempt to conserve resources and the possibility that resource conservation is the epiphenomenal result of sharing and other cultural practices. Our attempt was to test the former hypothesis. While other hunter-gatherer societies practice techniques of resource conservation, the Ache share their resources widely but in their other resource acquisition behaviors show no evidence of any regard for resource conservation.

Yesner points out, however, that the current situation of the Ache may not tell us very much about the importance of resource conservation in the past. Is it possible that the Ache do not need to conserve resources because they hunt less and therefore place less pressure on animal resources in their environment? Data we are currently collecting in the field suggest that this is not the case. Although our sample is still small, the Ache appear to be encountering and harvesting fewer large animals, particularly peccaries, in 1984 than they did in 1981–82. They also complain that they and their Paraguayan neighbors have killed off most of the peccaries in nearby areas.

Yesner also suggests that the Ache, because of their mission attachment, may have a greater need to exploit animal resources intensively when they forage. However, if this is the case, one would expect them to demonstrate more concern for resource conservation now than in the past. We see no evidence of this. We accept his point that the Ache may be adjusting their yields to *minimum* animal production levels rather than to *average* maximum sustained yields. The problem here is that the Ache hunt long hours every day when they forage (Hill and Hawkes 1983, Hill et al. 1984), and we have never observed them to pass by an animal resource unless they felt that the pursuit would be too difficult (e.g., not taking monkeys in thick-tangled forest) or that they could obtain higher returns from hunting something else (e.g., leaving monkeys when another hunter has found peccaries). In sum, Ache males are persistent, highly motivated hunters. If, as Harris suggests, the purpose of food sharing is to sap individuals' motivation to intensify their food acquisition efforts, it does not seem to be very effective in the case of the Ache. While we agree with Yesner that the matter is not settled, we do think that our data

cast some doubt on the hypothesis that egalitarian food sharing is practiced by hunter-gatherers *in order to* conserve resources.

Finally, Yesner suggests that our rejection of group selection is based upon logical grounds rather than empirical data and that the force of this logic depends upon one's acceptance of the theoretical assumptions of modern evolutionary theory. This assessment is correct: our empirical data are equally consistent with both group- and individual-selection interpretations. The last 20 years of ecological research on nonhumans suggests that individual- (and inclusive-) fitness models have greater explanatory power than those based upon group selection, but this does not a priori mean that the same will be true of research on humans. The resolution of this issue awaits further research and theoretical debate. We are, however, less concerned with the adoption of evolutionary ecology as a research strategy for anthropology than with the use of uniformitarian models and quantitative methods for testing alternative explanatory hypotheses about human behavior. We hope that the present research has made some contribution toward meeting this need to develop and test general models of human behavioral variability.

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