

Interhousehold Meat Sharing among Mayangna and Miskito Horticulturalists in Nicaragua

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Abstract Recent analyses of food sharing in small-scale societies indicate that reciprocal altruism maintains interhousehold food transfers, even among close kin. In this study, matrix-based regression methods are used to test the explanatory power of reciprocal altruism, kin selection, and tolerated scrounging. In a network of 35 households in Nicaragua's Bosawas Reserve, the significant predictors of food sharing include kinship, interhousehold distance, and reciprocity. In particular, resources tend to flow from households with relatively more meat to closely related households with little, as predicted by kin selection. This generalization is especially true of household dyads with mother-offspring relationships, which suggests that studies of food sharing may benefit from distinctions between lineal and collateral kin. Overall, this analysis suggests that exchanges among kin are primarily associated with differences in need, not reciprocity. Finally, although large game is distributed widely, qualitative observations indicate that hunters typically do not relinquish control of the distribution in ways predicted by costly signaling theory.

Keywords Social network analysis · Cooperation · Food sharing · Kin selection · Reciprocal altruism · Tolerated scrounging

Although other primates share food, the diversity and complexity of food sharing in human societies is remarkable. In recent years, evolutionary anthropologists have devoted considerable attention to food sharing because of its hypothesized importance to the evolution of unique human traits, including a suite of distinctive life history traits (Hawkes et al. 2000; Kaplan et al. 2000) and a hypersocial cooperative orientation (Isaac 1978).

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While there has been renewed attention on the conflicts of interest between mothers and fathers (Hawkes and Bliege Bird 2002; Gurven and Hill 2009) and the potential contributions of their offspring (Kramer 2004), evolutionary researchers have occasionally taken for granted that transfers of food within households or families are based on overlapping interests and a division of labor that results in positive outcomes for genetically related kin (Kaplan and Gurven 2005). By contrast, transfers of food *between* households have received relatively more attention, and there is considerable debate about the evolutionary advantages of such food sharing.

Some recent empirical studies in preindustrial settings have indicated that interhousehold food sharing is biased toward kin (Gurven et al. 2000b; Patton 2005; see also Ziker and Schnegg 2005). Other studies, however, have not necessarily revealed such biases (e.g., Hames and McCabe 2007). Meanwhile, recent theoretical contributions have featured arguments based in part on the importance of reciprocal altruism as the evolutionary mechanism that results in sharing between households (Gurven and Hill 2009). In an important paper that is consistent with predictions derived from game theory (Wilson and Dugatkin 1991), Allen-Arave et al. (2008) demonstrate that reservation-dwelling Ache households share primarily with closely related households that are likely to reciprocate, not the kin who would benefit the most from donations of food. Similarly, Nolin (2011) concludes that reciprocal altruism is the motivation for food sharing in Lamalera and, like Allen-Arave et al. (2008), argues that kinship might be important primarily as a factor in partner choice.

Because the predictions of food sharing hypotheses frequently overlap, evolutionary researchers have increasingly used multivariate statistical approaches to compare the effects of several predictor variables. This paper applies the logic of the Allen-Arave et al. (2008) approach to a study of food sharing among the Mayangna and Miskito of Nicaragua. Using permutation-based multivariate statistics that are common to social network analysis, this study addresses the relative importance of kinship, reciprocity, need, and distance to patterns of interhousehold food exchange. This analysis is used to test the explanatory power of multiple evolutionary models of food sharing, including kin selection, reciprocal altruism, tolerated scrounging, and costly signaling.

Evolutionary Models of Food Sharing

Kin Selection

Models of kin selection are based on the insight that biological kin have a greater likelihood of sharing alleles by common descent. This probability, labeled r , is Wright's (1922) coefficient of relatedness. Hamilton (1964) showed that altruistic behaviors toward kin can be favored by natural selection when $br > c$, where b is the fitness benefit to the recipient and c is the cost to the donor. Because it is difficult to measure the long-term fitness effects of giving and receiving food, most anthropological studies of food sharing assume that these effects are essentially equal for all individuals and that closer kin should therefore be favored over more

distant kin. As an exception to this generalization, Allen-Arave et al. (2008) provide an analysis that incorporates differences in short-term need as well as relatedness. More broadly, Rogers (1993) notes that, given the choice between potential recipients of equal relatedness, donors should preferentially target individuals of greater reproductive value, such as reproductive-age adults instead of postreproductive individuals or children.

Kin selection is a recognition that individuals can accrue inclusive fitness benefits through their own reproduction, or *direct fitness*, as well as the reproduction of related individuals, or *indirect fitness* (Griffin and West 2002). The distinction between lineal and collateral kin is rarely highlighted in anthropological studies of food sharing, however (Getty 2004). In other words, analyses based solely on the coefficient of relatedness make no distinction between offspring ($r=0.5$) and full siblings ($r=0.5$), for example. Since the intrahousehold distribution of food is generally dominated by exchanges between parents and offspring, analyses that do not make this distinction may overlook the corresponding importance of these lineal relationships in sharing between households.

Reciprocal Altruism

Trivers (1971) proposed that altruistic behavior may be evolutionary advantageous if recipients of altruism reciprocate in the future. In terms of food sharing, this reciprocity may serve to reduce the risk of resource shortfalls for both parties (Winterhalder 1986). A central prediction of reciprocal altruism is that sharing within a dyad should be “contingent” on past and expected transfers (Gurven 2006). In other words, there should be a correlation between the bidirectional flows within the dyad. The transferred amounts do not need to be precisely equal as long as the value of a future return exceeds the marginal value of the shared resource (Gurven 2004b). For example, highly productive households that generally give a disproportionate amount may benefit greatly when they receive food during periods of acute need (Gurven et al. 2000a). Given that “need” may vary dramatically over time, researchers question how much contingent reciprocity to expect during relatively brief ethnographic studies (Bliege Bird et al. 2002), but temporal discounting reduces the value of resources that are reciprocated at progressively later dates.

Although tests of contingency are important to tests of reciprocal altruism, such analyses do not account for the possibility that donors of food are repaid in other currencies, including child care, agricultural labor, political support, and other goods and services. While such “trades” do not reduce the variance in the intake of specific food resources, they may reflect and promote specialization of labor (Winterhalder 1986). Trade is probably common in many ethnographic settings, but the difficulty of converting all goods and services into a common currency has hindered the evolutionary analysis of trade.

Tolerated Scrounging

Compared with hungry individuals, relatively sated individuals may gain less value from consuming additional portions of food. Given this difference in the marginal

valuation of resources, the owner's expected benefit of keeping the resource may be less than the cost of defending the resource from motivated "scroungers," for whom portions of the resource are worth considerably more. Food transfers that are motivated by the relatively high costs of defense exemplify "tolerated scrounging," originally called "tolerated theft" (Blurton Jones 1987). In other words, this model predicts transfers from the "haves" to the "have-nots," with little expectation of reciprocity. Tolerated scrounging may be especially common when individuals possess large, asynchronously acquired resources, such as large game animals (Winterhalder 1996; Tucker 2004). Importantly, contests over resources are not expected to be violent. Instead, the threat of gossip or emotional discomfort may be sufficient to prompt transfers.

Costly Signaling

Based on the "handicap principle" of Zahavi (1977), applications of costly signaling theory to human food sharing assert that donors are broadcasting important information about themselves. An important insight of costly signaling theory is that both signalers and observers may benefit from the transmission of this information, perhaps by allowing observers to gauge the signaler's desirability as a mate or an ally. For example, hunters might convey information about their skill as hunters by harvesting prey that are difficult or costly to kill and then distributing the meat to a broad audience (Bliege Bird et al. 2001). To offset the costs associated with the signal, it may be beneficial for foragers to broadcast the signal widely. Costly signaling theorists have therefore suggested that foragers benefit by relinquishing control of their acquisitions in front of large audiences, such as collective feasts (Smith and Bliege Bird 2000).

Study Site

Created in 1991, the Bosawas Biosphere Reserve is inhabited by two indigenous groups, the Miskito and the Mayangna (Stocks 2003). Although Miskito and Mayangna ethnicity and language remain distinct, there has been considerable intermarriage and acculturation between the two populations, and the ecological strategies of the two groups are generally indistinguishable. The forested region in which they live is relatively remote, as there are few roads within the reserve itself. Although the communities are largely self-sufficient, consumer goods such as machetes, clothing, soap, coffee, flashlights, and candles are imported into the reserve along the major waterways. Since the missionary activity of the early twentieth century, religious activities revolve around either Catholic or Moravian churches (Stocks 1996). Virtually all communities have primary schools with local teachers employed by the national government, but secondary schools are usually located only in communities with populations exceeding about 500 people.

The nuclear family household is the basic unit of production and consumption. Descent is traced bilaterally, and although there appears to be an uxorilocal bias for first marriages, there are no clearly established postmarital residence rules (von Houwald 2003). A typical household consists of a nominally monogamous husband

and wife and their offspring, often including children from previous relationships. Young couples commonly live with one set of parents until they have children, and single mothers likewise live in their parents' household. Postreproductive widows and widowers usually live with one of their children.

Swidden agriculture provides the majority of calories in the diet, and staple crops include bananas, plantains, manioc, corn, rice, and beans. Dietary protein requirements are satisfied primarily through the consumption of hunted game, fish, and domestic animal products. Hunting is almost exclusively a male activity, and hunting implements include dogs and .22-caliber rifles (Koster 2008a). Common prey types include agoutis, pacas, nine-banded armadillos, collared peccaries, white-lipped peccaries, and tapirs (Koster 2008b). The harvest of fish peaks in the dry season (January–May), when the clear water allows men to use the bow and arrow, lures, and scuba masks and crossbows (Koster 2007). In the rainy season, both males and females commonly use fishhooks. The Mayangna and Miskito also keep domestic animals, most notably cattle, pigs, chickens, and turkeys. Cattle are viewed as a store of wealth and are therefore consumed only rarely. Panning for gold is the leading source of cash income (Stocks 1996).

Men generally assist with the butchery of animals larger than about 20 kg, but virtually all other butchery is handled by women and girls. Portions of meat are most frequently distributed to other households after the initial stages of butchery, such as the gutting of the animal. Sometimes portions are handed off to recipients at the owner's household. More commonly, children carry portions to the recipients' households. As in Nolin's (2011) data, multiple adult members of the possessing household can influence the sharing decisions; neither the acquirer of the resource nor the person in charge of butchering and cooking assumes full control of the distribution. Meanwhile, although there is a clear understanding that the meat will be shared by all members of the receiving household, donors sometimes identify the primary target of the distribution. For example, fishermen would occasionally report their intention to give some of the fish to a specific individual in another household. When asked, children bringing meat to another household could also indicate the intended recipient. These reports were among the first indications of the importance of mother-offspring relationships. In a nearby Miskito community, Helms (1971:105) similarly reports that mothers are the most frequent recipients of shared food.

This study was based in two communities, Arang Dak and Suma Pipi, located approximately 1 km apart on the Lakus River. During the study period, there were about 190 permanent residents in Arang Dak, living in 25 households. Suma Pipi is smaller, with about 70 residents in 10 households. Research in Arang Dak began in mid-August 2004. The initiation of research in Suma Pipi was delayed for various reasons, and uninterrupted data collection did not begin there until mid-December 2004. Data collection in both communities ended in early September 2005.

Determining the boundaries of a social network is important, but not always straightforward. Despite constituting two separate communities, both Arang Dak and Suma Pipi are considered part of the same network in this study because (1) separated by only one kilometer, the two communities are closer than many households in food sharing studies conducted in a single community (e.g., Patton 2005; Nolin 2011), (2) the next closest community is more than 4 km downstream, and (3) most households in Suma Pipi have multiple

close kin ties with households in Arang Dak. Also, all matrix-based analyses were repeated on the 25 households in Arang Dak with few noteworthy differences in the results (see [Electronic Supplementary Material](#)).

Finally, Hames (2000) emphasizes that predictions about food exchanges must account for the adaptive problem that sharing is designed to meet, whether risk-reduction, specialization through trade, the costly signaling of phenotypic quality, etc. It is therefore important to note that, although hunted game and fish represent the leading sources of dietary protein in Arang Dak and Suma Pipi, the daily per capita consumption of game (0.08 kg/day) and fish (0.03 kg/day) is low in comparison with other neotropical societies (Koster 2007). For example, the corresponding per capita estimates for the Yanomamo are 0.25 kg/day of game and 0.13 kg/day of fish (Chagnon and Hames 1979). The Piro (Alvard 1993) and the Waorani (Yost and Kelley 1983) also consume more than twice as much game as the participants in this study. Yet, compared with Arang Dak and Suma Pipi, the per capita consumption of fish and game is substantially lower in other nearby communities in the Bosawas Reserve, seemingly without dire nutritional consequences (Williams-Guillen et al. 2006). Because dietary protein can be acquired through other means, including grains and domestic animals, this setting apparently does not require a steady supply of fish and game, which may indicate that risk-reduction reciprocity is not the primary purpose of exchange.

Methods

Data Collection

Data on interhousehold food exchanges come from daily food consumption forms, which were kept in the household and completed each morning by local research assistants with input from female household heads about foods consumed in the previous 24 h. Originally designed as a way to gauge the nutritional importance of fish and game, these forms do not provide data on the consumption of foods with little dietary protein, such as bananas, plantains, or manioc. Food types on the form include hunted game, fish, pork, poultry, beef, milk, eggs, beans, maize, and rice. When participants reported the consumption of these foods, the assistants documented the source of the food. If it was acquired from outside the household, the assistant would determine if it was purchased or gifted, the identity of the person who provided the food, and an estimated amount (pounds of meat, number of eggs, etc.). Purchases were usually made with Nicaraguan currency, but this category also includes trades of meat for specific amounts of other goods or services, such as a bag of oranges or 7 h of agricultural labor. The remainder of this paper focuses on gifted food, and purchases will be addressed in a subsequent publication.

For three reasons, the analysis in this paper focuses only on animal-based products, not grain crops. First, unlike animal-based resources, gifts of grains frequently entailed specific expectations of in-kind repayment at a later date. In other words, such exchanges were essentially loans until the recipient household was able to harvest their own crops. Second, unlike grains, animal-based resources cannot be stored indefinitely, and third, they provide a comparable macronutrient profile.

Although informants are generally very good at estimating the amount of exchanged resources, the analysis in this paper is based on the number of consumption events, or “hits” (Kaplan and Hill 1985). In this study, a “hit” is counted for each day on which a resource is consumed. Although this method overlooks possible variation in the size of food transfers, larger portions of meat are typically consumed over multiple days, thus counting for multiple hits. Therefore, as with the Ache data (Kaplan et al. 1984), there is a correlation between hits and package size.

Reflecting the beginning of data collection in Suma Pipi, this analysis includes only exchange data from January 1 to August 31, 2005. This interval encompasses the dry season, when fishing returns are highest. Hunting returns exhibit much less seasonality (Koster 2007).

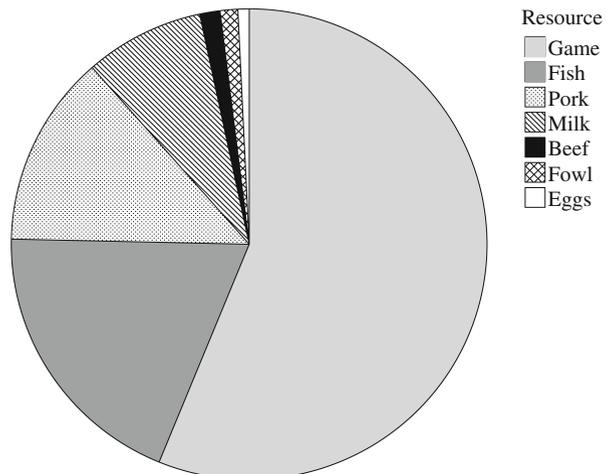
Other sources of data complement the data on interhousehold exchange. A GPS unit was used to map the locations of households. Throughout the study period, local research assistants documented the harvest of all fish and game, including the identity of the acquirer (see Koster 2008b for a full description of these methods). Genealogies to at least the grandparental generation were used to calculate purported genetic relatedness between all individuals using DESCENT, version 0.2.0.2 (Hagen 2005).

Characterizing the Exchange Dataset

The exchange data were organized as a matrix with 35 rows and 35 columns, yielding a total of 595 unique dyads. Cell i, j represents the cumulative gifted hits from household i to household j during the 8-month study period. Gifted portions of hunted game constitute approximately 56% of the hits in the sample, while fish and pork also represent a large proportion of the exchanges (Fig. 1). Because milk and eggs contribute a relatively small proportion of hits in the sample, the subsequent discussion will sometimes include the term “meat” instead of “animal-based products,” but the inclusion of milk and eggs is implied.

Two new households formed in March and April, respectively. Another dissolved in June. Other families were away from the community for brief periods. To account for

Fig. 1 Proportion of different animal-based products in the asymmetric exchange matrix



these absences, the values in the original exchange matrix were divided by the number of days that both households in the dyad were present in the community. This calculation produces a matrix in which the values represent the number of hits per day exchanged between households in the dyad. This latter matrix, hereafter called the “asymmetric exchange matrix,” is the outcome variable for many of the analyses in this paper.

Analysis

Tests of all matrix-based correlations were conducted using the quadratic assignment procedure, or QAP (Hubert and Schultz 1976). Because they account for the statistical non-independence associated with dyadic data, QAP analyses are becoming increasingly common in research by evolutionary anthropologists (Alvard 2003, 2009; Ziker and Schnegg 2005). Such tests begin by calculating the correlation coefficient between the corresponding cells of two matrices. The rows and columns of the original matrix are then randomly permuted many times (5,000 in this case) to determine how many of the permuted matrices result in an effect size greater than the observed correlation, which is reported as a proportion. A low proportion ($p < 0.05$) indicates a relationship between the matrices that is unlikely to occur by chance. Similar permutation-based techniques are used in multivariate QAP regression, or MRQAP. In this paper, MRQAP is based on the semi-partialing method of Dekker et al. (2007), as implemented in UCINET (Borgatti et al. 2002). Standardized coefficients in MRQAP models are interpreted like those in conventional multiple regression models. Table 1 includes a description of several predictor variables included in the analysis. Other analyses in this paper, including the tests of general household-level characteristics, rely on conventional inferential statistics, including nonparametric tests.

Table 1 Description of main-effects predictor variables

| Variable | Description |
|------------------------------------|---|
| Reciprocity | Transpose of the outcome variable matrix |
| Interhousehold distance | Distance in meters between households in the dyad |
| C:P ratio imbalance | Difference of the C:P ratio between households A and B |
| Per capita fish and game imbalance | Difference between households A and B in their daily per capita harvest of wild fish and game |
| Mother-offspring tie in dyad | Symmetrical dummy matrix to denote presence of a mother-offspring relationship between members of households A and B |
| Full sibling or father tie in dyad | Symmetrical dummy matrix to denote presence of a relationship with relatedness coefficient of 0.5 in household dyads that do not have mother-offspring ties |
| Close kin tie in dyad | Symmetrical dummy matrix to denote presence of a relationship with relatedness coefficient of at least 0.25 but less than 0.5 in household dyads |
| Other recognized kin tie in dyad | Symmetrical dummy matrix to denote presence of a relationship with relatedness coefficient of at least 0.10 but less than 0.25 in household dyads |

Researchers have used the closest genetic tie between households as a measure of dyadic relatedness (Gurven et al. 2000b, 2001; see also Patton 2005). Relying only on the coefficient of relatedness, however, does not allow for the possibility that mother-offspring relationships might be qualitatively different than relationships between full siblings or between fathers and offspring. Because much of the rhetoric in these communities centers on the importance of caring for one's mother, these relationships merit a distinction in the analysis. Accordingly, a symmetric matrix with a dichotomous dummy variable was created to denote the 21 dyads that include mother-offspring ties.

Other kin relationships are similarly represented by dummy variables. A matrix represents the 54 household dyads that include either father-offspring ties ($n=3$) or full siblings (but not mother-offspring ties). A third symmetric matrix denotes the 88 dyads in which the closest tie is at least 0.25 but less than 0.5, and a final matrix includes a dummy variable for the 87 dyads in which the closest tie is less than 0.25 but greater than 0.10. This latter category includes most cousins ($r=0.125$), which is generally the limit for the Mayangna and Miskito to recognize another individual as kin (von Houwald 2003).

Household "need" can be analyzed in a number of ways. An analysis presented here replicates the use of consumer-to-producer (C:P) ratios by Hames and McCabe (2007). The number of producers in a household was based on 82 days of scan-sampling time-allocation data (Koster 2007). Men and women were analyzed separately; the average labor time of individuals between the ages of 20 and 50 was assigned a value of 1.0, and individuals older and younger than this interval were considered fractional producers depending on how closely they approximate this standard. Estimates of consumption were derived from Kaplan's (1994) among the Machiguenga and Kramer's (2002) among the Maya.

In addition, because approximately 75% of the hits in the asymmetric exchange matrix are either fish or hunted game, a comparison of the household harvests of these resources provides insight into the relative value of animal-based foods to each household. The harvest data were used to calculate each household's daily per capita acquisition of fish and game. Subtracting the per capita harvest of household B from the per capita harvest of household A provides the imbalance measure used in this analysis.¹

Paralleling Allen-Arave et al. (2008), the categorical kinship variables are interacted with the per capita fish game harvest imbalances as a measure of kin-directed altruism. Additional terms are created by interacting the categorical kinship variables and the transpose of the asymmetric exchange matrix, which provide a test of kin-directed reciprocity.

In network terms, the cumulative total of hits per day given to other households is the "out-degree" and the total received from other households is

¹ Because households that harvest relatively little fish and game may compensate by increasing their production of domestic animals, it would be preferable to incorporate such production into the measure of household need, but the weights of slaughtered domestic animals were not recorded. However, there appears to be little relationship between a household's per capita acquisition of fish and game and the household's per capita consumption of domestic animal products, as measured in the cumulative hits per person per day of household-produced beef, pork, fowl, eggs, or milk (Pearson's $r=0.26$; $p=0.13$; $n=35$). To the extent that household consumption is an index of household production, this result suggests that households do not compensate for the relative lack of fish and game by focusing on domesticated animals.

the “in-degree.” The difference between these variables provides a measure of *general balance* (Hames 1987).

Finally, the *specific imbalance* refers to the difference of gifts per day from household A to household B minus gifts per day from household B to household A.²

Results

Many of the relationships between the asymmetric exchange matrix and predictor variables are evident in a visualization of the exchange network (Fig. 2). The results of the statistical analysis and interpretations are continued below.

Kinship

When the categorical relatedness variables are included in an MRQAP regression with the asymmetric exchange as the outcome variable ($R^2=0.25$), the dummy matrices with mother-offspring ties ($\beta=0.49$; $p<0.001$), father-offspring or sibling ties ($\beta=0.17$; $p<0.001$), other close kin ($\beta=0.11$; $p<0.001$), and other recognized kin ($\beta=0.08$; $p=0.01$) are all significant predictors.³ Because kin are likely recipients of exchanged meat, and because the volume of exchange is greater among closer kin, these initial results are consistent with kin selection. Based on the strength of the effects, however, it is reasonably clear that there are qualitative differences between mother-offspring ties and other close kin ties. Exchanges are particularly common in dyads with mother-offspring relationships.

To examine whether resources tend to flow primarily from the mother’s household to the households of her children or vice versa, the specific imbalance between these dyads is calculated by subtracting the transfers per day from the offspring’s household from the transfers per day from the mother’s household. The average imbalance is -0.025 ± 0.129 transfers per day, suggesting a slight tendency for resources to flow from the households of offspring to mothers’ households. The standard deviation is large, however, indicating that there is no clear pattern of directionality in dyads with mother-offspring relationships. A plot of the relationship between the specific imbalance of transfers per day and the per capita fish and game imbalance suggests that resources tend to flow from households that have relatively more fish and game to those with less, which may or may not be the mothers’ households (Fig. 3).

At the level of the household, in a multiple regression model with “out-degree” as the outcome variable ($R^2=0.65$; $p<0.001$; $n=35$), the household per capita harvest of fish and game is a significant predictor ($\beta=0.80$; $p<0.001$), but the overall average household interrelatedness to the other 34 households is not significant at conventional levels ($\beta=0.11$; $p=0.31$). That is, the presence of kin in other

² Hames (1987) calls this measure *specific balance*, but this study uses the terminology of Allen-Arave et al. (2008).

³ By contrast, using the closest interhousehold tie ($r=0.36$, $p<0.001$) accounts for less of the variation in interhousehold exchange. Average interhousehold relatedness, the measure used by Allen-Arave et al. (2008), is a marginally stronger predictor ($r=0.41$, $p<0.001$), apparently because 16 of the 20 most closely related households using this measure include mother-offspring relationships.

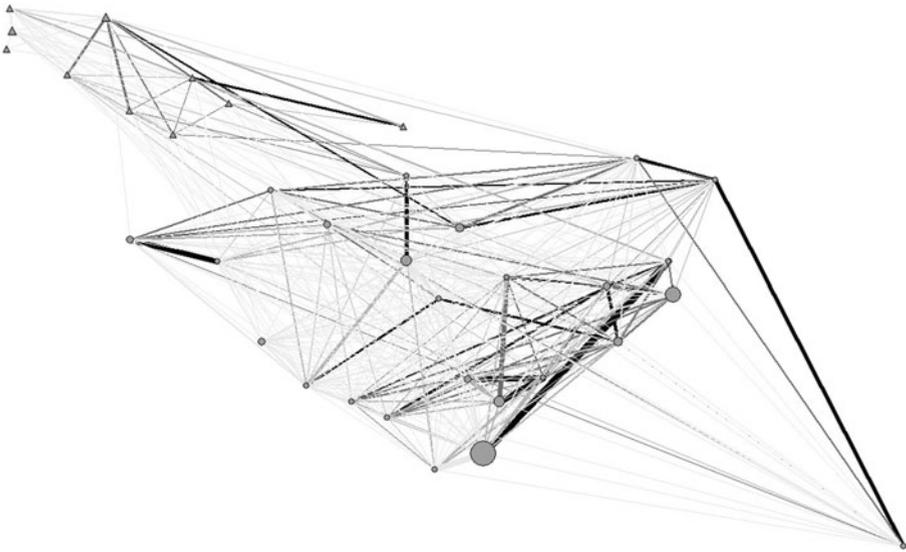


Fig. 2 A spatial visualization of the exchange network. The thickness of the line between nodes (i.e., households) represents the cumulative volume of hits per day exchanged between the dyad. Black lines denote dyads with mother-offspring relationships, dark gray lines indicate dyads with full siblings or father ties, medium-gray lines represent dyads with other close kin ties, and light gray lines denote dyads without close kin ties ($r < 0.25$). The size of the node varies proportionally with the household's per capita harvest of fish and game. Circles denote households in Arang Dak and triangles denote households in Suma Pipi. Within each community, the geographic representation of households is spatially accurate (the household on the lower right is located across the river from all other households in Arang Dak). To facilitate visualization, however, the distance between the communities has been artificially reduced by approximately 700 m

households appears to exhibit little effect on a household's overall propensity for sharing after controlling for variation in household harvests. This result is noteworthy because, holding other variables constant, kin selection predicts that households with fewer kin in the network should retain proportionally more meat for themselves, but the data do not support this prediction.

Reciprocity

There is a significant correlation between the asymmetric exchange matrix and its transpose ($r = 0.24$, $p < 0.001$). This result indicates that the number of hits per day from household A to household B is positively correlated with the number of hits per day from household B to household A.

For the 35 households in this sample, there is little relationship between out-degree and in-degree (Pearson's $r = -0.17$; $p = 0.34$). In other words, households that give more overall do not necessarily receive more. Using the terminology of Hames (1987), there is little general balance. When considering only exchanges between the 25 households in Arang Dak, however, there is a significant negative correlation between out-degree and in-degree (Pearson's $r = -0.56$; $p = 0.004$; $n = 25$). That is, households that give a lot in this community tend to receive less overall than households that give little.

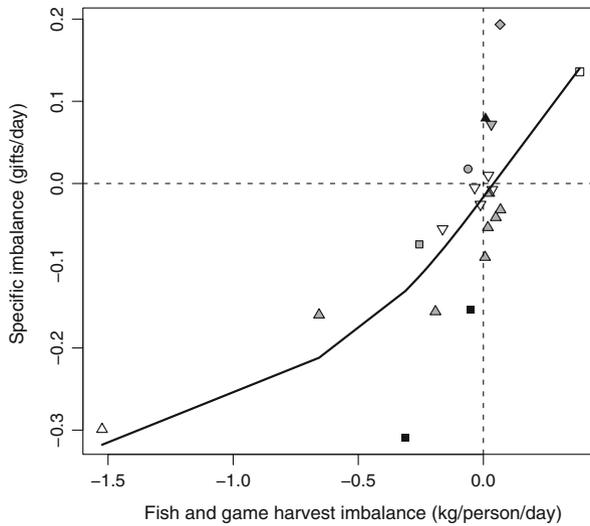


Fig. 3 In dyads with mother-offspring relationships, the specific imbalance in meat exchange is plotted against the per capita fish and game harvest imbalance. For both variables, the values for the offspring households are subtracted from the values for the mothers' households. Each of the 10 households in which mothers reside is represented by a unique symbol, and some appear multiple times to represent multiple lineal ties between households. *Gray symbols* represent households in which mothers remain married to the fathers of their offspring living in other households. *Black symbols* are households in which mothers are remarried to men who are not the fathers of their offspring in other households. *Open symbols* represent households in which the mothers are widows living with adult offspring. The scatterplot has a superimposed spline, which was fitted in R (R Development Core Team 2009) using the `smooth.spline` function with default settings

Distance

There is a significant negative correlation between the asymmetric exchange matrix and the distance between the households ($r=-0.28$, $p<0.001$). That is, as distance between the households decreases, there is more sharing between the households.⁴ Notably, although closely related households often live in close proximity, it is evident in the visualization that there are many exceptions to this generalization.

Need

There appears to be little relationship between the asymmetric exchange matrix and the difference in household C:P ratios ($r=0.002$; $p=0.50$). That is, resources generally do not flow from households with relatively more producers to households with relatively more consumers.

⁴ When a dummy matrix of shared community membership is included in a multivariate QAP regression model with the distance matrix, both the dummy variable ($\beta=-0.39$, $p=0.01$) and distance ($\beta=-0.66$, $p<0.001$) are significant predictors. Yet the amount of variance explained by this multivariate model ($R^2=0.08$) is essentially identical to the variance explained by distance alone ($R^2=0.08$). The results are not presented in this paper, but the dummy matrix of shared community membership was initially included as a predictor in all of the multivariate models presented below. Although this variable was a significant predictor, it typically altered only the standardized parameter estimates of distance as a predictor variable. The interpretation of all other variables remained unchanged.

There is a significant positive correlation between the asymmetric exchange matrix and the per capita fish and game imbalance ($r=0.23$; $p<0.001$). That is, households that acquire relatively more fish and game tend to give resources to households with comparatively little.⁵

At a general level, among the 35 households, there is a significant positive correlation between the household's daily per capita harvest of fish and game and both its out-degree (Spearman's $\rho=0.73$; $p<0.001$) and the number of households to which it gave during the study period (Spearman's $\rho=0.66$; $p<0.001$). In other words, productive households tend to give away relatively more meat and they at least occasionally distribute it to many other households. However, there is relatively little relationship between the household's daily per capita harvest of fish and game and either in-degree (Spearman's $\rho=-0.17$; $p=0.32$) or the number of households from which gifts were received (Spearman's $\rho=-0.07$; $p=0.71$). This result suggests that the households producing the least amount of meat do not necessarily receive more donations, nor do they receive from a broader range of donors.

MRQAP Analysis

To investigate the relative effects of kinship, distance, and need, the significant bivariate predictor variables and several interaction terms are included in a series of MRQAP models (Table 2). Although AIC (Akaike 1974) comparisons are not possible with randomization tests such as QAP, R^2 provides a measure of model fit. All of the models are significant at $p<0.001$.

The importance of mother-offspring relationships is evident in all of the models. In addition to the sustained importance of the main effect across models, the interaction effect of the dummy variable for mother-offspring relationship by the imbalance in acquired fish and game confirms the inference from Fig. 3 that, in such dyads, meat tends to flow according to differences in household supplies. By extension, there is little reciprocity in such dyads, as revealed in Model C by the negative effect of the mother-offspring relationship by reciprocity interaction term. In Model D, controlling for the fish and game imbalance in these dyads reduces the strength of this negative effect, but the parameter estimate remains significant and it appears that reciprocity does not characterize exchanges between households with mother-offspring ties.

In terms of other kin relationships, the models suggest that households with full-sibling or father-offspring ties are more likely recipients of meat exchanges. By contrast, households with other close kin ties appear to receive only slightly more meat than a household without close ties to a donor's household. The main effect for more distant kin (e.g., cousins) is not significant in any of the models, which indicates that kin relationships may be relatively unimportant once the closest tie in a dyad is less than 0.25.

⁵ Whereas the household C:P ratio exhibits little relationship to the per capita harvest of wild game (Pearson's $r=-0.03$; $p=0.89$; $n=35$), there is a significant negative correlation between household C:P ratio and the per capita harvest of fish (Pearson's $r=-0.45$; $p=0.007$; $n=35$). In general, households with numerous young children harvest relatively little fish whereas households with primarily older children and adults harvest relatively more.

Table 2 Results of MRQAP regression, including standardized parameters

| | Model A | Model B | Model C | Model D |
|--|---------|---------|---------|---------|
| R^2 | .325 | .470 | .357 | .474 |
| Reciprocity | .03 | .24*** | .10*** | .21*** |
| Interhousehold distance | -.16*** | -.13*** | -.14*** | -.13*** |
| Per capita fish and game imbalance | .23*** | .08 | .25*** | .08 |
| Mother-offspring tie in dyad | .44*** | .35*** | .56*** | .39*** |
| Other 0.5 tie in dyad | .12*** | .09*** | .10** | .09** |
| Close kin tie in dyad | .05* | .04* | .03 | .04* |
| Other recognized kin tie in dyad | .03 | .02 | .01 | .01 |
| Interaction mother tie by imbalance | | .41*** | | .38*** |
| Interaction other 0.5 tie by imbalance | | .11** | | .12** |
| Interaction close kin tie by imbalance | | .10** | | .11** |
| Interaction other kin tie by imbalance | | .16*** | | .18*** |
| Interaction mother tie by reciprocity | | | -.22*** | -.05** |
| Interaction other 0.5 tie by reciprocity | | | .03*** | .01 |
| Interaction close kin tie by reciprocity | | | .05 | .02 |
| Interaction other kin tie by reciprocity | | | .07** | .06 |

An asymmetric matrix of exchanged animal products is the outcome variable

P-values: * <0.05; ** <0.01; *** <0.001

As with mother-offspring dyads, however, households with other kin ties receive greater amounts of meat when they harvest less fish and game than the donor's household, as seen in the positive and significant effects of the imbalance-related interaction terms in Models B and D. In other words, there appear to be need-based exchanges among households with kin ties. Although these interaction effects are not as pronounced as the need-based exchange in dyads with mother-offspring ties, these results provide additional support for kin selection. It is noteworthy, however, that exchanges among more distant kin seem to occur primarily when there is a disparity in household supplies of meat, and because the inclusive fitness benefits to the donors are reduced relative to transfers to closer kin, the strength of this interaction term suggests that scrounging might characterize aspects of these exchanges.

Although there is clearly little evidence for reciprocity in dyads with mother-offspring ties, is there evidence for kin-directed reciprocity among households with other kin ties? The two positive and significant coefficients for the reciprocity-related interaction terms in Model C could be consistent with this interpretation. Although significant, the effects of these interaction terms are relatively weak, however, and none are significant in Model D. Furthermore, the inclusion of these terms in Model D does not discernibly enhance the model fit when compared with Model B. In general, the results therefore suggest that exchanges among kin are primarily associated with need, not reciprocity.

In Model A, reciprocity exhibits little effect on the model, apparently because dyads with mother-offspring ties are characterized by substantial imbalances in

exchange. When interaction terms are added that account for these imbalances, reciprocity is a significant and positive predictor in Models B, C, and D. This result indicates that household dyads tend to exhibit relative balance in their exchanges, which provides support for reciprocal altruism.

After controlling for need-based transfers to kin in Models B and D, the harvest imbalance between households does not exhibit a significant effect. These models therefore provide little evidence of tolerated scrounging among distantly related or unrelated households (i.e., Wright's $r < 0.10$). To the extent that exchanges between neighbors might reflect tolerated scrounging, however, the consistently significant relationship between interhousehold distance and exchange could be interpreted as evidence for tolerated scrounging (see Patton 2005).

Discussion

Kinship

The overall pattern of exchange indicates that exchanges of meat are particularly common between mothers and their offspring in other households. To a lesser extent, donors preferentially give meat to other kin, particularly kin with little meat themselves. Households that live nearby are also preferred targets, as are households that reciprocate with comparable amounts of donations. To varying degrees, these results provide support for several evolutionary models of food sharing, including kin selection, reciprocal altruism, and tolerated scrounging. Of these models, however, kin selection consistently receives the strongest support.

Perhaps the most interesting result from this analysis is the importance of mother-offspring relationships. Whereas previous analyses of food sharing have not distinguished lineal and collateral kin, these findings suggest that this distinction may be important. As noted previously, transfers among lineal kin in the same household are almost taken for granted, but the same pattern also seems to characterize interhousehold transfers at this study site.

Among the Mayangna and Miskito, it is common for a woman's older offspring to form new households nearby. Although older sons sometimes marry and form new households in this way, it seems particularly likely for older daughters. These related households then comprise a "super-household" with similarities to comparable clusters of households among the Piro and Machiguenga (Gurven and Kaplan 2006).⁶ These super-households cultivate fields in close proximity, and the sharing of agricultural labor is common. In the community, these households do not necessarily cook and share communal meals, but they seem particularly likely to share food at meals (see also Ziker and Schnegg 2005). For example, children were sometimes observed eating food at their grandmother's house while their mothers were temporarily away from the community.

As noted, there was not a clear directional pattern of exchange between households with mother-offspring relationships. The strength of the interaction term

⁶ Although households now maintain separate dwellings, Conzemiuss (1932) reports that the indigenous societies of the Mosquitia formerly used communal, multifamily houses.

“mother-offspring tie by harvest imbalance” in the multivariate models indicates that the difference in the respective supplies of meat is an important factor. In some cases, the mother’s husband is a productive hunter or fisherman, and portions of the meat are given to offspring and children in other households. In other cases, a son or son-in-law produces a lot of meat that is shared with the mother’s household, which may also include her dependent offspring. In both cases, the net effect is to reduce variance in meat consumption by members of the super-household. Because the primary beneficiaries of this arrangement may be either the grandchildren or younger siblings of the meat producer, the emergence and stability of such super-households merits additional attention in ongoing debates about the distribution of productive labor and specialization needed to support reproduction and cooperative breeding (Hrdy 2005; Kramer 2005).

Interestingly, whereas the intergenerational model of Kaplan (1994) suggests that the debts incurred by offspring are not repaid directly but rather redirected toward grandchildren, this study suggests that parents’ households are frequent recipients of meat even when there are no longer any dependent offspring in the household. The household that cumulatively receives the most gifts (0.56 hits per day) from households with mother-offspring ties consists of only three people: an elderly couple and their unmarried, childless, 29-year-old son. Their other seven living children are household heads in Arang Dak who share significant portions of meat with their parents and brother while seemingly forgoing opportunities to invest in close kin with greater reproductive value, namely their other siblings, nieces, and nephews, as well as their own offspring.

Reciprocity

Although there is little general balance, the significance of reciprocity in the MRQAP models that include the interaction terms provides additional support for the importance of contingent reciprocity among household dyads (Gurven 2004a). This study did not, however, match the findings of Allen-Arave et al. (2008) that contingent reciprocity is stronger among closely related households than among distantly related households. That is, unlike the Ache of Arroyo Bandera, the households in this study generally direct meat toward kin with little meat themselves rather than relatives that regularly reciprocate. This result is interesting given the many similarities between the two field sites. The communities are similar in size, for example, and the average interhousehold relatedness is comparable (0.02 ± 0.04 for the Ache, and 0.03 ± 0.05 for Arang Dak and Suma Pipi). Cultivated foods provide most of the calories in both settings, and although bananas and plantains (*Musa* spp.) are important only for the Mayangna and Miskito, the mix of root crops and grains is otherwise similar (Gurven et al. 2001; see Beckerman 1993 for a discussion of the variation in subsistence associated with the cultivation of *Musa* spp.).

The potentially important differences between the sites include the greater importance of fishing to the Mayangna and Miskito, apparently fewer unsuccessful hunting trips in Suma Pipi and Arang Dak, and greater market integration in Nicaragua. Perhaps most importantly, this analysis focuses only on animal-based resources whereas Allen-Arave et al. (2008) analyze all food exchanged between

households, and Gurven et al. (2001) report that meat exhibits less contingent reciprocity at Arroyo Bandera.⁷ Aside from this caveat, the differences between the studies provide a reminder that the food sharing literature lacks a conclusive theory to predict the relative strength of different mechanisms (e.g., kin selection vs. reciprocity) in different settings (Winterhalder 1997).

Finally, although there is little reciprocity among kin in this sample, perhaps gifts of meat are being repaid in another currency, such as vegetable foods or other trades of goods and services. Interestingly, whereas Gurven et al. (2004) report that putative biological relatedness is not associated with foraging partnerships in Arroyo Bandera (see also Alvard 2003), preliminary analysis suggests that the residents of Arang Dak and Suma Pipi primarily associate with members of closely related households on excursions away from the communities. Such associations may allow households that receive gifts of meat to repay their relatives in currencies that are ultimately more valuable than reciprocated meat, such as child care, loans of boats and subsistence technologies, agricultural labor, permission to cultivate fallow fields, and other kinds of food resources.

Tolerated Scrounging, Large Game, and Costly Signaling

Among kin, resources flow from households with relatively greater supplies of meat to households with relatively little. There is little evidence, however, that the imbalance in supplies is associated with transfers among household dyads that lack widely acknowledged kin ties. Furthermore, as seen in the household-level analysis, the apparently neediest households do not receive a disproportionate amount of the distributed meat. These results are not consistent with predictions of tolerated scrounging, at least among distantly related or unrelated households. It may be that, unlike Winterhalder's (1996) marginal model, the neediest households do not have the same ability to coerce portions from owners of meat. Alternatively, if possessors of meat are ceding portions in order to be repaid in other currencies, then perhaps the neediest households have less to offer in terms of exchangeable resources, prospective mates, or enhancements to reputations.

On the other hand, the household-level analysis indicates that households with relatively more meat initiate more exchanges overall and give at least occasionally to a higher percentage of other households. These results reflect the distribution of large game, which is shared widely, as predicted by marginal models. For example, after hunters harvest adult tapirs, which weigh approximately 180 kg, portions might be given to at least 20 other households, including unrelated households with little ability or propensity to reciprocate in kind. In general, relatively few households harvest large game, in large part because dogs that can track and corral the reserve's large ungulates are rare.

In part because of the importance of large game to Plio-Pleistocene hominins, the distribution of large game has received considerable attention as a likely candidate

⁷ Kaplan and Gurven (2005) briefly comment that the Ache data from Arroyo Bandera reveal greater imbalances (i.e., less reciprocity) among kin of disparate ages, such as parents and offspring, than among kin of similar ages, such as siblings. This result more closely conforms to the results of this study and its emphasis on mother-offspring relationships, but these data from Arroyo Bandera have apparently not been published.

for alternative models of food sharing, particularly costly signaling or “showing off” (Hawkes et al. 2001). Costly signaling hypotheses are not specifically tested in this analysis, but the overall evidence for the importance of signaling is not especially compelling in comparison to some of the better-developed examples in the literature (e.g., Bliege Bird et al. 2001). With a few minor exceptions, for instance, Mayangna and Miskito hunters generally focus on prey types that are in the optimal diet set (Koster 2008a; Koster et al. 2010). Also, upon harvesting animals, hunters rather unambiguously retain control of the distribution of the meat, and this control is a component of tolerated scrounging but not costly signaling models (Smith 2004; see Bird and Bliege Bird 2010 for a description of foragers who relinquish control of distributions).⁸ Tapirs are often butchered on the riverbank, for example, and hunters direct shares to specific recipients. These distributions almost invariably attract a large crowd of onlookers, and although demands for shares are typically not aggressive or articulated aloud (cf. Peterson 1993), the onlookers’ expectant expressions may impose an emotional cost that motivates the transfers according to tolerated scrounging. On the other hand, these crowds may provide hunters the opportunity to gauge the interest of prospective buyers of the meat.⁹

Although distributions of large game do not necessarily adhere to predictions of costly signaling, a recent analysis of informant rankings indicates that there is widespread consensus on the relative hunting abilities of men in Arang Dak (Koster et al. 2010). In other words, hunters do not necessarily have to relinquish control of their harvests for reputations as hunters to be established. Distributions of hunted game may be meant to signal not hunting ability but prosocial intent, which could result in greater assistance in times of need (Gurven et al. 2000a; see also Wiessner 2002). This hypothesis is beyond the scope of this paper, however.

Summary

This study provides support for multiple evolutionary models of food sharing, most notably kin selection and reciprocal altruism, while the distribution of large game resembles tolerated scrounging more than costly signaling. Overall, animal-based resources tend to flow from households with comparatively large amounts of meat to closely related households with little meat, and this is especially true of household dyads that include mother-offspring relationships. This result closely conforms to predictions of kin selection, and this study therefore contributes to broader debates about the importance of intergenerational food transfers to the evolution of unique life history traits in humans.

As a cautionary note, however, it is important to acknowledge that even closely related individuals can exhibit evolutionary conflicts of interest (Trivers 1974).

⁸ In this study, the exception to this generalization involves communal meals at church-related activities, to which hunters sometimes donate meat while other families contribute other kinds of foods, firewood, candles, coffee, etc. However, these activities are relatively rare and probably account for less than 5% of the total meat consumption during the study period.

⁹ Approximately 41% of the purchases of tapir meat were preceded or accompanied by gifted portions to the same household, which raises the intriguing possibility that these gifts serve as “free samples” that subsequently motivate purchases of larger portions.

Transfers of food to needy kin do not necessarily have to satisfy the conditions of Hamilton's rule if donors give food partly to avoid the costs of defending it from their relatives. In other words, tolerated scrounging is possible among kin, and the challenge of distinguishing kin selection from tolerated scrounging requires additional attention from evolutionary researchers.

More generally, the emphasis on kin selection in this analysis should not obscure the importance of other reasons for sharing food. In this study, the households of prolific hunters with relatively few kin in the community tend to share meat as frequently as those with abundant kin, and even households with broad kin-based networks often share meat with distantly related households when they have large quantities of meat. These results are a reminder that people who have food resources likely have multiple motives for giving portions to different recipients. Although researchers may emphasize one model over others, a number of multivariate analyses have demonstrated support for multiple evolutionary models of food sharing (Allen-Arave et al. 2008; Gurven et al. 2000b, 2002; Nolin 2011; Patton 2005). It will be a significant challenge for evolutionary researchers to develop a multicausal theory of food sharing that, in a broad variety of ethnographic settings, successfully predicts the relative effects of variables such as relatedness, reciprocity, and both short-term and long-term disparities in need.

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