WHY DO FORAGERS SHARE AND SHARERS FORAGE? EXPLORATIONS OF SOCIAL DIMENSIONS OF FORAGING

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ABSTRACT

Commonly studied hunter-gatherer traits, such as grouping and sharing, may require special attention when self-selection introduces bias into typical analyses. We therefore re-examine forager sociality by asking a series of nested questions: (1) To what extent are foraging groups random samples from the larger population? (2) What social and economic factors might explain the composition of foraging groups? (3) If certain groups of individuals preferentially forage together, do these same groups also preferentially share with each other when resident at their permanent settlement? (4) To what extent can we understand behavior in the foraging context without consideration of other contexts in which individuals live and work, and vice versa? Among the Ache of Paraguay, we show that foraging treks are not representative of the larger population, individuals vary in the kinds of treks in which they participate, and those who tend to share together at the reservation are more likely to forage together on trek.

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1. INTRODUCTION

The Ache of Paraguay came to epitomize hunter-gatherer generosity i after Kaplan and Hill (1985) first showed quantitative evidence that their food sharing patterns in the early 1980s were highly egalitarian. The Ache ethnographic case study has since been invoked to support both popular and academic accounts of the origins of human altruism and cooperativeness (Cosmides & Tooby, 1992; Kameda et al., 2002; Miller, 2000; Ridley, 1996). Kaplan and Hill (1985) showed that roughly 90% of small and large-sized game items were given to members of other families. While non-meat items such as fruits, palm fiber, and honey, were shared less widely, on average an impressive 60% of these foods were given away to non-family members. Subsequent analyses have shown that over the course of two-week long foraging trips, members of each family give some food to members of every other family about 97% of the time (Gurven et al., 2001, 2002). Conversely, sharing patterns observed among Ache while resident at a horticultural colony are less egalitarian than those observed during foraging trips. While the Ache of Arroyo Bandera still give away significant portions of game and cultigens (90 and 76%, respectively), single meat and non-meat resources are given to an average of only 3 (out of a possible 23) other families (Gurven et al., 2001). Over the duration of a four-month study, a single family shared roughly 75% of its food production with only three other families.

The Ache are well aware of the differences in sociality, sharing, and lifestyle while foraging versus while resident at the reservation. Many have commented on the difficulties of receiving shares in the large reservation population, and attest to the more desirable sub-group clustering of smaller sharing networks. Consistent with these views, explanations for the different sharing patterns in both contexts include a combination of ecological and social factors (Gurven et al., 2002). First, resources consumed at Arroyo Bandera are more predictable, and do not require substantial cooperation in their production. Second, the number of potential recipients is much greater in Arroyo Bandera than in typical foraging camps. Third, living in wooden houses spaced about 100 meters apart allows for more privacy than the typical spatial structure of foraging camps.

Studies of modern foragers are our best source of direct information on behavior, economy, and social life of hunter-gatherers, both present and past. Although the Ache are one of few groups who were full-time foragers up until recently, detailed studies of them were done only after contact and subsequent settlement. Foraging and sharing patterns have been studied in the context of temporary foraging trips and horticulture-based settlements, and these two contexts have mainly been described in isolation. Explicit consideration of how prior or expected future associations with the same people in one context may influence relationships in the other has not directly entered any analysis or discussion. It is important to recognize that all observed foraging trips, during which sharing and production data were collected, were temporary excursions leaving from and returning to a permanent residential colony. Hence, all inferences about food production, distributions, activity budgets, grouping, and group foraging efforts during foraging trips take as given the number and composition of trip members. The lack of independence between life in the forest and life at the reservation raises several important questions about interpretations of behavior within each context, but especially about the foraging context, which figures so prominently in evolutionary anthropology.

This paper therefore considers aspects of Ache grouping patterns, foraging behavior, and sharing partnerships by addressing a series of nested questions. We ask: (1) To what extent are foraging groups random samples of the larger population? How do certain individuals and groups of individuals self-select to forage together? Is the bias in observed foraging groups relevant to inferences about foraging-related behavior? (2) What economic and social factors might explain the patterns of social interactions in the forest? Are the observed sizes and composition of groups more consistent with the goal of maximizing the rate of food acquisition, or of something different, such as social prestige? (3) If certain groups of individuals preferentially forage together, do these same groups also preferentially share with each other at the reservation? To what extent does such a relationship reflect underlying social networks based on the benefits to cooperating with specific others? (4) If foraging and sharing partnerships are significantly correlated, then is the commonly reported pattern of communal sharing in the forest merely a consequence of extensive cooperation among groups of families back at the reservation? Would a more random sampling of individuals during foraging trips result in a less egalitarian sharing pattern? Conversely, we could also ask whether foraging partnerships lead to preferential sharing and tighter social networks at the reservation. We explore these questions involving foraging and sharing relationships by analyzing data on the composition of foraging treks of 23 Ache men leaving from the Arroyo Bandera settlement from 1995 to 1999, and on sharing behavior of these men and their families at Arroyo Bandera in 1998.

These questions are not limited to the Ache, nor to interpretations of food sharing patterns; they are general questions that are relevant for all anthropologists who make inferences about behavior, preferences, norms, and culture based on naturalistic observations of individuals. First, they recognize that inferences made about foraging-related behavior based on research among groups of individuals who are no longer full-time foragers may require special consideration. Most current (and future) studies of foraging behavior are done with living people who derive substantial nutrition from non-wild foods, market-derived foods, and government subsidies. Many of these people now live in larger communities with relatively close proximity to markets, roads, missions, and colonies. Instead of concluding that studies among foraging groups with mixed economies are at best misguided, and at worst, completely inadequate for attempting to understand foraging-based adaptations (e.g. Schrire, 1984), we argue in this paper that relatively recent behavior (e.g. farming, reservation life) can provide an additional source of variation that is useful for testing behavioral ecological models. For example, because the Ache now live on reservations, a day spent in the forest with others is the result of a conscious decision to leave the reservation and forage with others. Thus, foraging partnerships in the modern Ache context may reveal as much, if not more, about foraging partner preferences than if the Ache were constrained to forage everyday.

Second, agent-based models of social behavior often emphasize aspects of local ecology that affect costs and benefits of different strategies, but analyses rarely consider the actions and strategies of other individuals (as well as the history of interactions with those individuals) as part of that local ecology. The inclusion of others' actions in shaping ego's optimal strategy set, or the notion of frequency-dependency, has long been recognized by game theorists and foraging theory specialists as a potentially significant influence on individual behavior (e.g. Jochim, 1988; Maynard Smith, 1982). However, empirical investigations of human behavior have often ignored many aspects of the social context, such as potential partner characteristics, cooperative or pro-social tendencies in others, coordinated divisions of labor, and behavioral strategies and abilities of other group members. Rather, stable characteristics such as biological kinship have dominated analyses of social behavior. This neglect of the larger social and historical context is because simple behavioral ecological models (especially foraging models) have mainly been applied to non-social animals, and therefore ignore these complexities. Incorporation of frequency-dependent behavior into general foraging models adds considerable complexity and intractability (Giraldeau & Caraco, 2000). Nonetheless, we will not be able to explain the abundant exceptions and outliers observed when testing simple foraging models against empirical data on humans (e.g. Hill et al., 1987) unless we explicitly consider important aspects of frequencydependent decision-making, and characteristics of social partners.

2. STUDY POPULATION: THE ACHE

Much has been written over the past twenty years about Ache foraging behavior (Hill & Hawkes, 1983; Hill et al., 1987), demography and life history (Hill & Hurtado, 1996), and food sharing patterns (Gurven et al., 2000, 2001, 2002;

Kaplan & Hill, 1985). The Northern Ache were full-time hunter-gatherers until the 1970s, at which time they were peaceably settled in several permanent communities where horticulture was introduced. The post-contact reservation period has seen high population growth due to high fertility and declining infant mortality. The majority of the calories consumed in the current Ache diet are derived from cultivated crops, including sweet manioc, corn, rice, and peanuts. They domesticate small animals such as chickens, and several individuals even have cows. Horticultural and domestic animal production is confined primarily to nuclear and extended families, as male heads of households clear and burn their own fields, and all family members weed and harvest.

The Ache spend up to 25% of their time in the forest on trek, where the diet consists mostly of wild game (especially nine-banded armadillos, pacas, and brown capuchin monkeys), honey, palm fiber, and seasonal fruits. In contrast to the horticulture-based economy of the reservation, men's foraging often involves a high degree of cooperation with each other, although both men and women often coordinate behaviors when on trek (Hill, 2002). Women gather palm fiber, larvae, and fruits along with children, and sometimes in small groups with other women. When groups of men forage together, they usually trek in a solitary manner but within earshot of each other in case one of them calls for help during an encounter. Other men are often called to assist in the pursuit of monkeys, pacas, and peccaries (*ibid*. Hill & Hawkes, 1983), although Ache do not usually begin their days in pursuit of specific animals. Although the degree of cooperation required for acquisition varies across resources, residential foraging groups involve a much greater level of coordination of group member activity than encountered at the reservation.

Anecdotal observations during foraging trips support the notion that current foraging trips are markedly similar to those during the 1980s in terms of foraging and sharing behavior. However, two changes deserve mention. First, hunters often eat portions from their own kills, contrary to the tacit cultural taboo that previously denied hunters this benefit. Second, white-lipped and collared peccaries and coatis have declined in daily contributions to the game portion of the diet. Armadillos, pacas, and capuchin monkeys are now the top three sources of animal protein (Hawkes et al., 1982; Hill & Tikuarangi, 1998). Peccaries, coatis, and monkeys are usually acquired by coordinated groups of men, pacas are sometimes acquired by several men, while armadillos are easily caught by solitary hunters. More detailed comparisons between forest and reservation contexts can be found in terms of diet and time allocation (Hawkes et al., 1987), demography (Hill & Hurtado, 1996), and food production and sharing (Gurven et al., 2002).

This paper refers to the Ache living in the Arroyo Bandera settlement. Arroyo Bandera was founded in 1980 when a group of Ache left the older Chupa Pou

settlement to accept the offer of a Protestant mission to live on the edge of a Guarani Indian reservation administered by that mission (Hill & Tikuarangi, 1998). It is located a short distance (6 km) from the Mbaracayu Reserve, a \sim 600 km² region where the Ache forage. In 1998, there were 117 permanent residents comprising 23 nuclear family-based households living in Arroyo Bandera. Families live in small wooden houses, arranged in a circle around a soccer field. Food preparation and consumption occurs either in exposed kitchen areas in front of the houses, or more rarely, inside the house. Every adult man possesses a bow and several arrows in his house, and is therefore equipped to go hunting on any given day.

3. METHODS

3.1. Foraging Trip Composition

A continuous census of foraging trips has been collected by an Arroyo Bandera resident, Felipe Jakugi, since 1995, as part of a hunting sustainability project organized by one of the authors (Kim Hill). A "foraging trip" or "trek" can be defined as any departure from Arroyo Bandera to the Reserve for extracting food resources from the environment. For each trip, Jakugi recorded the length of the trip in days, the identity of all hunters on the trip, and all game items killed by each member on each foraging day. Neither the presence nor the identities of women and children were recorded for these trips. Men usually travel alone on singleman, single-day trips, while women and children are more likely to participate on foraging trips that last at least several days. The sample we used for this paper includes 753 foraging trips involving 30 men in Arroyo Bandera between September 1995 and December 1999. This sample represents 6,365 man-days of foraging over a period of 52 months, which constitutes about 14% of all days. Comparison of Jakugi's notes with those of others present on several of those trips, and of other researchers present in Arroyo Bandera in 1998, reveals that Jakugi's data are reasonably accurate.¹

3.2. Food Transfers

Food sharing data were collected in the Arroyo Bandera reservation over 55 sample days between February and May 1998. A total of 380 complete (mass = 1030 kg) and 635 incomplete (mass = 1247 kg) food distributions were sampled using a combination of focal-household cluster observations (87% of all distributions), focal-resource sampling (7%), and interviews (6%).

Focal-household cluster observations were three-hour observation blocks of all food distributions, consumption, and production events of all members of two or three households. Each household was sampled in this manner for an average of 56 hours, yielding 1294 house-hours of observation for all 24 nuclear familybased households in Arroyo Bandera. For each food distribution, Gurven and a research assistant (W. Allen-Arave) recorded the donor, original acquirer (if different), recipients, total resource package size, and amounts given to each recipient. Amounts were either weighed using 10-kg and 25-kg Homs spring scales or counted (as in sticks of manioc), and then converted to kilograms or calories by using unit weight measurements of counted resources. Further details on sharing methodology are provided in (Gurven et al., 2001).

The sharing data are best analyzed at the level of the nuclear family, rather than the individual, because many foods are often shared by household members other than the acquirer. For example, hunters' wives may share portions of meat or stew, while kids may share oranges or manioc roots that their mother harvested. Food is freely shared within the household, and so sharing between two households occurs if any member in one family gives food to any member of another family.

Because the composition and quantity of sharing partnerships is of primary interest, rather than the overall levels of sharing *per se*, we focus attention on the percentage of food production each family gave to the nuclear family of each of the hunters. We examine the distribution of several resource categories – all food types pooled, cultigens, foraged foods brought back from treks, and market foods purchased from local merchants. There was not a sufficient sample of sharing events involving domesticated animals to warrant a separate analysis of these foods.

3.3. Analyses

We examine bivariate relationships between variables using correlations and linear regression. For multivariate analyses, we use path analysis and multiple linear regression. Path analysis is a method for exploring the relationship between foraging and sharing partnerships. Path analysis is useful for examining the relationship between two variables that are related to each other through a causal process involving other, usually co-dependent, variables (Gurven et al., 2000; Loehlin, 1987). We use path analysis to examine the relationship between the percentage of *A*'s foraging days spent with *B* and the percentage of *B*'s foraging days spent with *A*.² The other predictor variables included in this analysis include sharing of foraged foods and cultigens (where sharing is defined above), kinship (Wright's coefficient of relatedness with individual *B*) and household

proximity ("distance in meters to individual *B*'s house"). Kinship and proximity may be responsible for explaining the patterning of sharing and/or foraging partnerships, and so omission of these variables from our analysis could result in a spurious correlation between foraging and sharing partnerships where none exists.

The fact that food transfers are dyadic in the sense that any piece of food is transferred between only one donor and one recipient, while foraging treks are multi-individual activities, does not invalidate the comparison of our measures of sharing and foraging relations. Any single distribution can have n-1 recipients, just as any foraging trek can include n-1 other members. While the range of observed sharing and foraging partners may differ, the means and medians are similar (2 vs. 4 men, respectively), given the availability of 23 other men in the village. It is likely that individuals are more easily excluded from sharing distributions at the reservation than from participating on foraging treks in the forest, but this only makes our investigation of co-dependence between sharing and foraging relations more conservative.

4. RESULTS

We first present a general description of Ache foraging group sizes and composition. The second section examines social relationships among foraging group members. The third section describes Ache sharing groups at the reservation. The fourth section examines the relationship between foraging and sharing groups.

4.1. Foraging Trips

There were an average of 2.6 (S.D. = 2.2) men present per trip in the sample of 753 trips from 1995 to 1999, for a mean duration of 2.3 (S.D. = 2.5) days.³ A total of 41% of all trips were solitary trips (with 98% of these trips being single-day trips), while only 20% of all trips were multi-male and longer than three days. Table 1 presents the frequency of trips for each combination of trip duration and number of hunters. The mean length of multi-day trips was 3.2 days (S.D. = 3.0), with 3.8 men (S.D. = 2.3) present. It is apparent from inspection of Table 1 that larger groups of hunters go on longer trips (r = 0.46, p < 0.001). Little is known about how individual Ache men decide when and for how long to go foraging. Ache will often complain about "meat hunger" due to the relative scarcity of meat at the reservation, and this hunger may motivate a desire to forage. However,

									-												
	#Days									Total	%										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	23		
# Me	n																				
1	312	6																		318	42.2
2	101	21	3	8	7	1	4	3				1								149	19.8
3	48	14	16	8	11	6	2	3	1	1	1	1	1			1			1	114	15.1
4	18	6	12	10	6	8	1	1			2	1	1			1				67	8.9
5	12	3	1	8	5	2	4													35	4.6
6	3	1	6	3	4		1	1	2	1	3									25	3.3
7	4		5	1	3			1				1								15	2.0
8	1	2	4	1	4	1														13	1.7
9	1		1				1				1									4	0.5
10	1			1																2	0.3
11	1	1	1	1														1		5	0.7
12			1			1														2	0.3
13					1															1	0.1
14												1								1	0.1
15				1			1													2	0.3
16																				1	0.1
Total	502	54	50	43	41	19	14	9	3	2	7	5	1	0	0	2	0	1	1	753	
%	66.7	7.2	6.6	5.7	5.4	2.5	1.9	1.2	0.4	0.3	0.9	0.7	0.1	0.0	0.0	0.3	0.0	0.1	0.1		

Table 1. Frequency of Trips by Number of Hunters and Trip Length in Days (n = 753, Sept. 1995 to Dec. 1999).

there is no centralized decision-making institution for organizing trips. Sometimes small groups of men may loosely plan a trip, but plans often do not result in a coordinated trek. Some trips are planned somewhat secretly, by invitation only, and individuals discretely leave the reservation; other trips are publicly announced and discussed openly. Ache do not act as if certain group sizes are more desirable when foraging, even on extended trips, although pursuit group size may have an important effect on foraging return rates (Hill & Hawkes, 1983; McMillan, 2001). On both single- and multi-day trips, a greater number of hunters present on the trip is associated with a greater total quantity of meat calories acquired (r = 0.52, p < 0.0001; r = 0.55, p < 0.0001 for daily returns on single- and multi-day trips, respectively), although there is no relationship between the number of hunters and per-capita meat production (r = -0.02, p = 0.86; r = -0.09; p = 0.33).⁴

There is substantial variation across men in the number of foraging trips that each of them participated in, total days spent foraging in the forest, the mean number of other hunters present on trips (and the standard deviation), and the number and proportion of all foraging trips that were solitary excursions. Table 2 presents these

ID	Total# Trips	Total #Forest Days	Mean Trip Duration (Days)	Mean #Men Present	S.D. of Mean #Men	WTD #Men Per Trip	#Solitary Trips	Fraction Solitary
16	114	247	2.17	3.70	2.99	5.45	22	19.3
2	105	376	3.58	4.50	2.92	5.32	8	7.6
6	105	357	3.40	4.70	3.10	5.45	7	6.7
19	103	267	2.59	3.75	2.99	5.25	20	19.4
10	92	265	2.88	4.39	3.13	5.58	13	14.1
15	90	205	2.28	4.09	2.98	5.41	16	17.8
9	89	206	2.31	3.28	2.84	4.28	28	31.5
1	73	221	3.03	4.68	3.46	5.63	17	23.3
5	73	297	4.07	4.19	3.07	4.95	9	12.3
13	70	138	1.97	3.80	3.16	5.77	13	18.6
4	69	204	2.96	3.59	2.91	4.09	19	27.5
11	61	158	2.59	4.38	2.99	5.94	7	11.5
7	60	181	3.02	3.27	2.94	4.26	18	30.0
20	46	118	2.57	4.54	3.43	6.32	5	10.9
18	45	78	1.73	3.13	2.74	4.59	18	40.0
12	42	183	4.36	5.38	3.44	6.50	2	4.8
8	38	185	4.87	3.18	1.52	3.51	2	5.3
28	30	133	4.43	5.33	3.99	6.10	3	10.0
24	29	83	2.86	5.03	2.88	5.76	1	3.4
22	23	33	1.43	3.30	3.48	4.82	13	56.5
3	22	89	4.05	4.36	2.13	4.87	1	4.5
21	19	42	2.21	4.05	3.29	5.76	4	21.1
23	18	35	1.94	4.89	3.08	5.80	4	22.2
17	15	56	3.73	4.47	3.68	6.29	4	26.7
27	15	48	3.20	6.47	3.80	7.35	1	6.7
25	12	39	3.25	4.75	3.89	5.49	1	8.3
26	7	19	2.71	4.43	3.55	4.95	1	14.3
14	6	11	1.83	6.33	4.46	6.64	1	16.7
30	3	9	3.00	5.33	1.15	5.33	0	0.0
29	2	12	6.00	4.50	3.54	6.58	0	0.0
Max	114	376	6.00	6.47	4.46	7.35	28	56.5
Min	2	9	1.43	3.13	1.15	3.51	0	0.0
Mean	49	143	3.03	4.39	3.12	5.47	9	16.4
Median	44	136	2.92	4.41	3.09	5.47	6	14.2
S.D.	36	106	1.02	0.84	0.66	0.84	8	12.4

Table 2. Individual Foraging Group Patterns for 30 Men.

Note: Each ID refers to a different hunter, ranked from those who participated in the most to the least number of trips. *Mean # men* refers to the average number of men present on a trip, where each trip is weighted equally; *WTD mean # men* weights each trip by its length in days; *# solitary trips* refers to the number of trips with no other men present; *fraction solitary* refers to the proportion of each hunter's trips that was solitary.

data and other summary statistics for the sample of 30 men. Again, these results show that men differ substantially in the number of days they leave the reservation to forage, and in the type of trips in which they are most likely to participate. Men spent anywhere from 9 to 357 days (2 to 114 trips) in the forest, with anywhere from 0 to 57% of the trips without other men present. However, on average, men went on trips that contained anywhere from 2.1 to 5.5 other men (2.5–6.4 if these means are weighted by trip duration). Men tend to vary most in the frequency of solitary hunting and hunting with one other man.

4.2. Predictors of Foraging Partnerships

Foraging in the forest is often viewed as a cooperative endeavor (Hill, 2002), even if the analysis of mean per capita return rates for meat production is not significantly related to the number of hunters present. A more salient benefit to group for aging is that the variance in production, and hence consumption, is lower with larger groups of hunters. Thus, traits of potential foraging partners may be important to consider in decisions about foraging group formation. Men often engage in activities that decrease their personal return rate, but increase the return rates of others, which makes sense only when there is pooling at the end of the day. Trust may therefore be an important characteristic of hunting partners. Men may prefer hunting with men of similar ages, either because these individuals tend to be closer friends, or because of preferences to forage with men in the same age cohort, especially when trust is greater among individuals in these categories. Men may also prefer to hunt with other men of similar hunting ability, or perhaps only with the best hunters. All of these predictions are consistent with the notion that hunters attempt to maximize the rate of meat production. Alternatively, if men wish to maximize prestige at the expense of caloric production, men should desire to forage with poorer hunters. These might include cohort members who are less able, or younger hunters who have yet to reach adult levels of hunting ability. In this way, good hunters when compared with poor hunters in Arroyo Bandera can gain signaling advantages by appearing more skilled (Wood & Hill, 2000).

To test these opposing predictions, we conduct a multiple regression analysis of foraging partnerships, which includes the difference in men's ages, and the difference in their ranked hunting ability (ranked from 1 to 5), while controlling for kinship and the spatial proximity of households, sharing of cultigens and foraged foods, and the total number of days spent in the forest. Foraging partnerships are measured by the percentage of forest days where another individual was present. The results of this analysis are reported in Table 3. The first column gives the partial estimates of the effects of each predictor variable (controlling for the other

Predictor Variable	Partial Estimate	Partial Std Est.
% <i>B</i> 's foraged food given to <i>A</i>	0.28^{**}	0.13**
% B's cultivated food given to A	-0.05	-0.02
Closest kinship between A and B	-1.5	-0.01
Distance in meters from A to B	-0.02^{*}	-0.08^{*}
% B's forest days spent with A	0.52^{***}	0.52^{***}
Age A – age B	-0.29^{***}	-0.34^{***}
Hunter ability A – hunter ability B	2.33****	0.31***
Total days A spent in forest	-0.02^{***}	-0.18^{***}

Table 3. What Influences the Total % of *A*'s Forest Days Spent With *B*?

Note: F-value = 34.43; p < 0.0001; $R^2 = 0.38$; df = 454.

*p-value < 0.05.

**p-value < 0.001.

***p-value < 0.0001.

variables) on the percentage of hunter *A*'s days spent in the forest with hunter *B*. The second column in Table 3 shows the standardized parameter estimates, whose magnitudes can be compared with each other to assess the relative importance of different predictors on foraging partnerships. Several results are noteworthy. First, the relative difference in age (age A - age B) is significant, such that older men are less likely to spend their foraging time with younger men, even after controlling for differences in time spent in the forest, and in ability. Second, poor hunters spend a greater percentage of their foraging days with good hunters, rather than vice versa, again controlling for differences in age and frequency of time spent in the forest. Third, the strongest predictor of *A*'s foraging with *B* is *B*'s foraging with *A*, controlling for all other predictors in the completed model that could potentially confound this effect. Fourth, the transfer of foraged foods is a significant predictor of foraging partnerships (see below), but is less important than the other significant predictors in the model. This multivariate model explains 38% of the variance in forest-days *A* spent with *B*.

4.3. Sharing

The diet at Arroyo Bandera consists of cultivated foods, foraged foods, marketderived foods, and domesticated animals. While the Ache at the reservation give a large percentage of their foods to non-family members, they tend to target distributions to only a few families. Figure 1 shows the percentage of food given to every other potential recipient nuclear family, with recipients ranked from those who received the most to those who received the least. A rank of zero refers to the



Rank of foraging companion or recipient family

Fig. 1. A Profile of Hunting and Sharing Partnerships From the Perspective of a Focal Hunter or Recipient Family. *Note:* Top line is the average percentage of a focal man's days in the forest spent with each other man, ranked from those with whom was spent the most to least number of days. Error bars signify a standard deviation unit. Bottom group of lines reflect the average percentage of a focal family's food production given to each other family, where recipient families are ranked from those who received the most to the least amount of all food, foraged foods, cultigens, and storebought foods. A rank of 0 refers to the percentage kept within the nuclear family of the acquirer. Error bars signify a single standard deviation unit for Total Food category.

percentage kept within the nuclear family of the acquirer. The sharing of cultigens, forest foods, market-derived items, or all foods combined, is marked by similar, steeply decelerating curves. A truly egalitarian sharing pattern would predict a relatively flat or slowly decelerating curve.⁵ However, we find that, on average,

82% of all cultigens, 81% of all store-bought foods, 68% of all forest foods, or 77% of all foods combined, are kept within the family or given to only four other families. The larger standard deviations in percentages of all food given to the first several ranked families (displayed as error bars in Fig. 1) indicate that families vary most in the extent to which they preferentially favor the few families who receive the most from them.

We can best summarize the distinguishing character of foraging and sharing partnerships in Fig. 1. This displays the percentage of *A*'s forest days spent with each other *B*, ranked from those *B*'s who were co-resident in the forest with *A* for the greatest to the least number of days. The top curve in Fig. 1 is less steep than the analogous curves for sharing in the bottom of Fig. 1, demonstrating that groups of individuals who forage together are larger, and have a more flexible composition over time, than those who share together at the reservation.⁶ Another way of describing the differences in foraging and sharing group sizes focuses on the total set of potential dyadic comparisons. Of all possible pairs of hunters that could be present on the same trip over the four-year period, only 7.6% never occurred, while 33% of all possible sharing pairs over a four-month period never occurred.

4.4. Foraging and Sharing Partnerships

If individuals who more frequently forage together more intensively share together at the reservation, we should expect significant correlations between the percentage of A's forest days spent with B and the percentage of B's food production given to A or of A's food production given to B. All else equal, according to nepotism based on kin selection, greater kinship affiliation should be associated with higher foraging and sharing affiliation. Greater spatial proximity should also associate with higher foraging and sharing affiliation if close proximity reduces important transaction or information costs, or if close proximity is itself a reflection of mutual affiliation. Bivariate analyses of the percentage of A's forest days spent with B show significant correlations with the percentage of B's foraged and cultivated food given to A (r = 0.47, p < 0.0001; r = 0.23, p < 0.05, respectively), as well as with the distance in meters between A's and B's house (r = -0.19, p < 0.0001), and the percentage of B's forest days spent with A (r = 0.21, p < 0.0001).^{7,8} No correlation is found with the percentage of B's market-derived foods given to A (or of A's given to B) (r = 0.11, p = 0.29; r = 0.04, p = 0.69), the percentage of A's cultivated food given to B (r = -0.01, p = 0.95), nor the closest kinship relation between members of A and B (r = 0.05, p = 0.31). While the percentage of A's foraged foods given to B is a (smaller) significant predictor of A's forest



Fig. 2. Path Model of Foraging and Sharing Partnerships. *Note:* Path analysis of the percentage of A's forest days spent with B as a function of the percentage of B's foraged and cultivated foods given to A, the percentage of B's forest days spent with A, the physical distance between the houses of A and B, and coefficient of relatedness (genetic kinship) between A and B. Solid lines refer to causal relationships, and broken lines refer to the correlations. The hanging arrows signify unexplained variance in the non-source variables.

days spent with *B*, it loses statistical significance when percentage of *B*'s foraged foods given to *A* is included in the model (p = 0.09).

We combine the significant predictor variables mentioned above in a path model to tease apart the relative effects of these co-dependent variables on the percentage of A's forest days spent with B. The path diagram of the causal model is illustrated in Fig. 2. The numbers on the arrows are standardized path estimates. Solid lines represent causal relationships, while dashed lines represent correlations. Sharing (the percentage of foraged foods and cultigens B gives to A), genetic proximity (closest kinship relation between members of A and B), geographical proximity (distance in meters between houses of A and B), and percentage of B's forest days spent with A are modeled as direct effects on the percentage of A's days spent with

B. Genetic and geographical proximity are source variables that also affect sharing and forest days *B* spent with *A*, and through these variables can have indirect effects on forest days *A* spent with *B*. Overall, the model is a good fit to the data $(\psi^2 = 3.70, p = 0.30; \text{Bentler's comparative-fit index (CFI)} = 0.995, \text{Bentler and Bonett's normed-fit index (NFI)} = 0.977).$

Several important results emerge from this analysis. First, geographical distance between households, the percentage of *B*'s forest days spent with *A*, and the percentage of *B*'s foraged food given to *A* each have similar significant effects on the percentage of *A*'s trip days spent with *B* (summed effect = 0.19, 0.18, 0.17 respectively). Notice that only half of the distance effect is direct, while the remaining indirect effect is due to the significant path estimates via the percentage of *B*'s trip days with *A*, and the percentage of foraged food *B* shared with *A*. Second, neither kinship nor the sharing of cultigens have any significant direct or indirect effects on foraging partnerships. Third, only 10% of the variance in the percentage of *A*'s trip days spent with *B* is explained by the inclusion of all these variables in the model. This contrasts with the 38% accounted for in the multivariate regression model described in the section on foraging partnerships.

5. DISCUSSION

Here we return to the four questions posed in the introduction.

5.1. Question 1: Non-Random Social Interaction

An important implication of this paper is that foraging groups are not random samples of the population, and that people often self-select into foraging groups based on a multitude of factors. That foraging trips are not random samples of the resident reservation group is also evident by comparing the censuses of foraging trips with those of the reservation source population. A comparison of the demographic composition of 18 foraging treks before 1986 and the Chupa Pou source population during this same period reveals a higher proportion of men and women older than 30, and a scarcity of teenagers and small children of both sexes on the foraging treks. This natural sampling bias raises important questions, including the extent to which observed levels of foraging effort, especially among teenagers, are typical of those during pre-contact times. Self-selection biases such as this one are under-explored realities that complicate interpretations of observed foraging or sharing behavior, or any naturalistically observed behavior for that matter.

Two examples illustrate our point. First, observational studies of foraging activities that are used to assess caloric return rates of foragers can lead to misleading estimates of foraging success rates and of abilities. This can happen if individuals selectively forage only during certain conditions, such as when weather is favorable, after receiving privileged information about animal locations from others, when opportunity costs are low, or when ability is sufficient. Second, if teenagers and children only increase work effort on foraging trips when the number of dependents is relatively high, then the low work effort of teenagers and children (and their low observed rates of caloric return) reported among groups such as the Ache and the !Kung may be more an artifact of the lower dependency characteristic of post-contact foraging trips rather than any inherent limitations in their foraging abilities. The reasons underlying the observed age-profiles of time spent in different foraging activities during childhood and adolescence has profound relevance for answering key questions concerning the relationship between big brains, delayed growth, and extended longevity - important traits that characterize our evolved human life history (see Bock & Sellen, 2002).

5.2. Question 2: Predictors of Foraging Partnerships

Although this paper was not meant to be an exhaustive study of the determinants of foraging partnerships, we have shown that several factors are important predictors of who forages with whom. Relative foraging ability, age, others' interest in foraging together, food sharing, and geographical proximity were all significant predictors of foraging partnerships. Although statistically significant in the multivariate models, sharing did not explain much of the variation in foraging partnerships. Another important finding was that biological kinship displayed no effect on foraging partnerships. This result is consistent with the absence of a kinship bias in sharing patterns during foraging trips (Gurven et al., 2001; Kaplan & Hill, 1985). The lack of a kinship bias in economic partnerships has also been observed among Lamalera whale hunting parties (Alvard, 2003), but was found among Alaskan whalers (Morgan, 1979). It is important to note that the effects reported here are significant even though we did not explicitly incorporate variation in foraging group sizes in the analyses. Foraging preferences are not always easily recognizable given the data on the composition of foraging trips, because the composition of any foraging trip (especially large ones) may be the result of many (often competing) preferences of multiple actors.

Almost half of all Ache foraging trips during 1995–1999 were solitary one-day trips. Does a decision to forage alone reflect a desire to avoid others? Alternatively, is the abundance of solitary trips linked to the decreased necessity for cooperation

during foraging trips (due to the importance of more easily acquired armadillos and decreased importance of peccaries and coatis in the diet)? Our suspicion is the latter. Indeed, only older and more skilled hunters participated in a greater number (but not proportion) of solitary excursions (r = 0.40, p = 0.05 for age; r = 0.59, p = 0.001 for ranked ability). Sharing behavior bears no relationship to the number or proportion of solitary trips, again suggesting that solitary foraging does not necessarily reflect a deficit of pro-social sentiment (p = 0.33, 0.34, 0.11 for three resource types and number of solitary trips; p = 0.12, 0.23, 0.85 for three resource types and proportion of solitary trips; df = 22).

Individuals who shared a greater proportion of cultigens, store-bought foods, or foraged foods at the reservation were also no more likely to forage in larger groups than those who shared fewer of these foods (p = 0.72, 0.31, 0.32 respectively; df = 22). Those who spent more time in the forest, however, were more likely to share more cultigens (r = 0.44, p = 0.04) and foraged foods (r = 0.46, p = 0.03) back at the reservation. Thus, skilled hunters who frequently hunt, and therefore are most likely to have animals to share back at the reservation, ascribe more to the traditional forest-sharing pattern when at the reservation. The only factors we found to correlate with average foraging party size were age and skill (which are themselves correlated, r = 0.53, p = 0.03, df = 23). Older and more skilled hunters are more likely to participate in trips with fewer total men (r = 0.52, p = 0.05 for age; r = 0.41, p = 0.05 for ranked hunting ability; df = 22).⁹ These same older and skilled hunters spent the greatest number of days in the forest on trek during the four-year sample period. The worst hunters, who tended to be the youngest men, participated primarily only on the large foraging trips. These trips tend to be the equivalent of open-invitation village parties in the forest.

Due to the high variance associated with Ache foraging bouts, which may vary on a day-to-day basis due to weather, or other subtle vagaries, perhaps the best way to compare hunting ability is when men hunt together on the same day. The fact that younger men hunt more with older, better hunters, and on larger trips where a larger audience is present, is inconsistent with the notion that men hunt primarily to garner prestige. Older and better hunters favor hunting with other good hunters, and of similar age, which is also inconsistent with gaining prestige, but rather is consistent with hunting as an efficient strategy for food acquisition.

It is important to mention here that any model of grouping patterns needs to consider the possibility for conflicts of interest among individuals (Smith, 1985). Ache will rarely go on trek for multiple days by themselves. Therefore, any extended trip requires coordinating other individuals to participate on a potential trek. At some point, member-joiner conflicts may arise, wherein group members may not wish to forage with others who wish to forage with them (ibid.). For example, more skilled hunters often forage with other skilled hunters, while poor hunters also prefer to forage with skilled hunters (p = 0.04, regression of percentage *A*'s forest days spent with *B* on the difference in ranked hunting abilities for *A* and *B*, where *A* is less skilled than B). Similarly, older individuals often forage with older men rather than younger men, whereas younger men show no age bias in their observed choice of foraging partners.

5.3. Question 3: Sharing and Foraging Partners

Our results show that pairs of families who share foraged foods together at the reservation also tend to participate in foraging trips together. This correlation was statistically significant even when controlling for other confounding associations, although reservation-sharing partnerships only explain a small proportion of the variance in foraging partnerships. This suggests that other factors, including those mentioned above, are important influences on foraging group composition. It is interesting to note that neither the sharing of cultigens, market-derived items, nor all foods combined were significant predictors of foraging partnerships in multivariate analyses. The fact that only sharing of foraged foods predicts foraging partnerships suggests that trade or turn-taking are unlikely social arrangements for obtaining meat among the Arroyo Bandera Ache. Furthermore, the lack of an effect of cultigen-sharing on the choice of foraging partners suggests that reservation sharing patterns, focusing mainly on cultigens, are not the reason that Ache engage in communal sharing during foraging excursions away from the community (see below).

5.4. Question 4: Foragers that Share, or Sharers that Forage?

If post-contact foraging treks have compositions akin to camping trips with friends, families, and age-mates, we might expect a higher level of cooperation in these trips compared with the typical mixed groups of pre-contact foraging bands. Does the correlation between foraging in the forest and sharing partnerships at the reservation force us to re-evaluate the appropriateness of using observed foraging or sharing patterns to make inferences about typical pre-contact forest behavior? While no data on pre-contact foraging or sharing patterns are available, many older Ache commonly report that widespread sharing has always been a core feature of forest life, even if estimated band sizes were larger during pre-contact times (McMillan, 2001). Personal observations of recently contacted groups by Hill in 1978 lend support to this notion. Additionally, preliminary analysis of unpublished sharing data collected during several foraging trips in 1998 revealed

few differences in food transfer patterns compared to the forest trips of the 1980s, and foraging groups have become even smaller during the past twenty years.

The dependence between foraging and sharing partnerships does not force us to conclude that sharing associations at the reservation are only a reflection of foraging partnerships in the forest. One of the strongest relationships that characterize sharing at the reservation is the correlation or contingency that exists between giving and receiving among pairs of families (Gurven et al., 2001, 2002). The significant contingency correlations of giving and receiving among the same pairs of families for all food, foraged food, cultigens, and store-bought foods - estimated using the percentages of food production each family gave to each other family over the duration of the sample period – remain significant. They are only slightly reduced in magnitude after controlling for the foraging associations among the same pairs of families in a multiple regression analysis (partial estimates = 0.35, 0.08, 0.33, 0.33, respectively; p < 0.0001, 0.0001, 0.05, 0.0001; df = 230). These results suggest that how much is given at the reservation depends on how much is received at the reservation, regardless of the amount of time both parties spent in the forest together. Thus, while time spent foraging on trek together may influence (or be a partial result of) social behavior at the reservation, sharing in the forest and at the reservation seems to be strongly determined by independent social factors occurring in these separate contexts.

It is also difficult to infer from the results reported in this paper that individuals of different households maintain a marked division of labor (cf. Chicchón, 1992). If *A* relies on *B* for access to meat, a large percentage of *A*'s forest days may be spent with *B* if access occurs in the forest context, whereas a low percentage of *A*'s forest days may be spent with *B* if *B* gives meat to *A* upon returning to the village. The fact that the transfer of cultigens and foraged foods from *A* to *B* were equally good predictors of the transfer of foraged foods from *B* to *A* (Gurven et al., 2001) suggests that, on average, the same sharing partners are called upon for access to different food types.

6. CONCLUSION

In modeling the decision for individual *A* to forage on any given day, one must not only consider certain frequency-independent factors such as weather conditions, time since meat was last eaten, number of offspring to feed, or own hunting ability, but also frequency-dependent influences such as the number and composition of individuals who have already committed to go foraging. The history of interactions with potential partners need also to be identified, such as whether these individuals are trust-worthy neighbors, age-mates, sharing partners, high or low producers, young women, etc. The relative importance of traits and circumstances may vary across individuals, and even within individuals over time, as reasons for foraging may incorporate both goals of food acquisition and prestige. Given the cluster of cues, factors, and coordination involved in the decision-making process regarding foraging group formation, it may not be surprising that a gross measure, such as "percentage of A's foraging days spent with B," does not reveal very tight foraging partnerships, and that the percentage of variation in foraging partnerships explained in our models is no greater than 38%. Strict economic considerations of group size might reveal optimal foraging party and pooling group sizes, but they do not consider the composition of those groups, nor how any particular group size is achieved. Even if A participates on a trip because B will be present, either A or *B* may also decide to participate on the trip because of meat hunger, good weather, appropriate seasonal time frame, information about certain profitable areas, in addition to the identities and characteristics of others expected to participate on the trip. Furthermore, others may choose to accompany A and B because A and/or B may be experienced, skilled hunters. Given that decisions to go foraging are rarely made simultaneously, the process by which group members or subsets of group members converge upon a specific course of action is an important area that deserves serious attention (see Alvard & Nolin, 2002).

Explorations of social dimensions of economic activities are a necessary companion to studies of the economic dimensions of social activities. Although grouping patterns are sometimes interpreted as providing useful information about species-typical or individual variation in pro-social or cooperative inclinations, straightforward interpretations often ignore the processes that produce grouping in the first place. If six individuals agree to forage because of a seasonal abundance in palm fruits, the harvesting of which does not require any coordination of individual actions, then the group foraging that follows is an example of simultaneous solitary foraging, rather than cooperative foraging (Giraldeau & Caraco, 2000). However, even simultaneous solitary foraging may require some additional explanations if, for example, fruit groves are dispersed, but individuals still choose to forage in the same patches.

During the five-year period when all foraging groups were recorded, the Ache did not leave the village to forage preferentially with kin. This means that the composition of foraging groups was not only as groups of closely related individuals, as described in many portrayals of typical hunter-gatherer foraging parties. Whether or not Ache foraging groups were more kin-based in the 1980s, when many of the foraging economics studies were conducted, is currently being investigated. Nonetheless, the fact that the Ache still share extensively in forest camps (and that kinship has no effect on sharing patterns in the forest – Gurven et al., 2002; Kaplan & Hill, 1985) supports the notion that close kinship is not

a prerequisite of effective cooperation. It may be that valued traits such as trust and hunting ability are not encountered in close kin, and so hunters may choose to forage with non-kin who do possess these traits. This reasoning is consistent with recent studies showing that even among chimpanzees, for whom it has often been assumed that kinship is the most important predictor of social affiliations, kinship plays only a secondary role in the development of grooming and spatial proximity, alliance formation, meat sharing, and boundary patrols (Mitani et al., 2000). However, we cannot rule out the possibility that some individuals may opt out of the forest-sharing network by choosing to hunt by themselves during singleday excursions, whereupon the foods they acquire are brought back to the village, and shared more restrictively with an evident kin bias in meat distribution.

Additional research is needed to explore the ways in which individuals form foraging parties, especially because most extant foragers and forageragriculturalists are central-place foragers who leave their larger, more permanent residential base to engage in temporary subsistence foraging. Decisions about group composition may interact in important ways with the kinds of activities and work effort decisions of those individuals while foraging. We have already mentioned many factors that may influence an individual's decision to forage and with whom to forage. Additional research is also needed to understand how an evolved pro-social psychology influences actual social behavior, given the ways that the dynamic socio-ecological context of an individual's local environment can structure the costs and benefits of cooperative behavior. For example, this paper reports that those who share food more generously do not forage in larger groups. Similarly, Hill and Gurven (2004) found that those who share generously did not behave any differently than less generous individuals in several economics games designed to measure individual cooperativeness. Understanding the multifaceted goals of individuals in specific situations, and how those goals trade-off in the context of limited time and resources, may provide important insight into explaining variability in social preferences and behaviors.

NOTES

1. For a sample of foraging trips in 1997–98, Jakugi underestimated the length of long trips, and missed several multi-day trips composed of older men (G. McMillan personal communication).

2. The values for each path are calculated by solving a set of simultaneous equations. Path values are expressed as standardized parameter estimates, where one standard deviation unit increase in the variable at the base of each arrow in the path diagram causes an increase in the variable at the head of each arrow equal to the parameter estimate given in standard

deviation units, controlling for all other effects in the model. One can assess the overall impact of *X* on *Y*(equivalent to the correlation between *X* and *Y*) by summing the direct effect of *X* on *Y*and the indirect effects of *X* on *Y*through intervening variables in the model. The path model was computed using the PROC CALIS procedure in SAS, which employs a maximum likelihood algorithm for estimating path coefficients (Hatcher, 1994).

3. If we weight this mean by the duration of each trip in days, we get an average of 3.8 men.

4. Correlations consider the number of individuals present on a trip, and this number squared, to consider a non-linear, quadratic relationship between number of hunters and productivity. The quadratic terms were not statistically significant (p > 0.3 in all cases).

5. Existing models of exchange which incorporate notions of marginal valuation would predict such an egalitarian distribution pattern only when the marginal value of food is approximately equal across families, as is the marginal cost to gaining access to food during distributions.

6. The slope of $\ln(\% A$'s days spent with *B*) is -0.17, and the slope of $\ln(\% A$'s forest food given to *B*) is -0.29. These slopes are the shape parameter in an exponential regression.

7. It may be argued that while "percentage of A's forest days spent with B" is a useful variable for comparing foraging partnerships across men, the large variation among men in time spent foraging can be misleading. We added the variable "number of days A spent in the forest" to control for variation in the denominators used in the calculation of the percentages. Controlling for time spent in the forest did not significantly change the magnitude nor significance of the correlations of percentage of A's forest days spent with B and percentage of all food B gave to A (r = 0.33, p = 0.02), percentage of B's foraged food given to A (r = 0.47, p < 0.0001), percentage of B's cultivated food given to A (r = 0.20, p = 0.07), and distance in meters between households (r = -0.20, p < 0.0001). The correlation between percentage of A's forest days spent with B and percentage of B's forest days spent with A actually increased, after controlling for the number of days A spent in the forest (r = 0.53, p < 0.0001).

8. The degree of association between individuals was also estimated using multidimensional scaling analysis (MDS), in addition to the path analysis described in the text. MDS analysis is a method commonly used to provide a representation of the strength of associations among a set of objects or individuals. The set of Ache men may be visualized as points in *n*-dimensional space, where the Euclidean distances between points correspond in a functional way to raw associations from an input matrix, and where the degree of fit is estimated by a stress criterion. The computed Euclidean distance between any two individuals is a measure of the strength of association between those individuals. Greater distances suggest weaker associations. The associations we consider in this paper include those related to foraging and sharing. The input matrix for foraging partnerships is the variable "percentage of all A's foraging days where individual B was present on the trip", computed for all A and B. Similarly, the input matrix for sharing partnerships is the "percentage of all B's (foraged) food given to the family of A". The MDS methodology therefore allows us to examine the relationships between pairs of individuals as a function of the derived Euclidean distances separating them, rather than from the raw input matrix data. MDS analyses were performed using PROC MDS in SAS V8.1.

The Euclidean distances that describe foraging preferences among all pairs of men are plotted against the distances describing sharing preferences among the same pairs. These distances are standardized to the maximum distances on each axis. We used seven dimensions for each of the MDS analyses to satisfy the criterion that the stress factor be below 0.1 Borgatti, S. (1992). ANTHROPAC 4.0 Methods Guide. Analytic Technologies, Columbia. A regression through these points reveals a positive, but weak, relationship between sharing of all food and foraging partnerships (estimate = 0.17, r = 0.14, p =0.003, n = 461). A similar relationship exists when considering the sharing of only forestderived foods (estimate = 0.19, r = 0.16, p < 0.001, n = 461). As described in the text, these results are similar to those obtained with regression and with the path model.

9. Correlations of age and average preferred foraging group size were taken from quadratic regressions.

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