ORIGINAL ARTICLE

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Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter–gatherers

Abstract The common occurrence of food transfers within human hunter–gatherer and forager–horticulturalist groups presents exciting test cases for evolutionary models of altruism. While kin biases in sharing are consistent with nepotism based on kin selection, there is much debate over the extent to which reciprocal altruism and tolerated scrounging provide useful explanations of observed behavior. This paper presents a model of optimal sharing breadth and depth, based on a general non-tit-for-tat form of risk-reduction based reciprocal altruism, and tests a series of predictions using data from Hiwi and Ache foragers. I show that large, high variance food items are shared more widely than small, easily acquired food items. Giving is conditional upon receiving in pairwise interactions and this correlation is usually stronger when the exchange of value rather than quantities is considered. Larger families and low producing families receive more and give less, consistent with the notion that marginal value may be a more salient currency than quantity.

Keywords Hunter–gatherers · Food sharing · Cooperation · Reciprocal altruism

Introduction

Reciprocal altruism theory (Trivers 1971) is often invoked to explain why unrelated individuals engage in various forms of intra-group cooperative behavior, such as blood regurgitation among vampire bats (Wilkinson 1988), egg trading among hermaphroditic fishes (Dugatkin and Mesterton-Gibbons 1996), predator inspection among sticklebacks (Milinksi 1987), allogrooming among impala (Hart and Hart 1992) and vervet monkeys (Sey-

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farth and Cheney 1984), and food transfers among brown capuchin monkeys (de Waal 1997), common chimpanzees (Boesch 1994; Mitani and Watts 2001), and humans (Kaplan and Hill 1985).

Although the particular mechanistic form of reciprocal altruism may vary for different behaviors, several essential components characterize all cooperative acts labeled as reciprocal altruism. First, reciprocal altruism must involve a cost to the donor and provide a benefit to the recipient. Second, a critical requirement of reciprocal altruism is that the donation of some benefit is given conditionally, i.e. on the receipt of future benefits from the current recipient (Rothstein and Pierotti 1988; Hill and Kaplan 1993). Thus, donors should withhold benefits from those who have defected on prior arrangements as a way of "punishing" the defection, and because it is likely that these "defectors" may defect again in the future at a cost to the donor. This conditionality or "contingency" can be difficult to observe and measure in natural populations,

In the typical tit-for-tat (TFT) versions of reciprocal altruism popularized by numerous modelers (e.g. Axelrod and Hamilton 1981; Axelrod and Dion 1988; Sigmund 1993; Nowak and Sigmund 1994), a lack of cooperation by an actor during a simultaneous encounter constitutes a "defection". In a sequential TFT game, defection is the lack of cooperation by X towards Y after an act of altruism by Y towards X. In applying reciprocal altruism theory to specific cooperative behaviors, what constitutes a defection is difficult to define because many cooperative acts often vary by degree (Frean 1996). Furthermore, especially among humans, there is no consensus about whether return benefits received after an extensive time delay are construed by actors or third-party observers as acts of defection, (partial) reciprocation, or perhaps reconciliation after an initial defection (see discussion in Gurven 2004).

One productive area of research on the evolutionary pathways to cooperation is the study of intra-group food transfers among hunter–gatherers and forager–horticulturalists (Winterhalder 1997). It is widely recognized that

Table 1 Definition of variables in the breadth–depth model. See text for details

Variable	Definition
$V(n)$	The return value from giving to n individuals
F	Package size of resource
A	Total amount given to all others
n	Number of recipients
k	Number of individuals who return to camp with food on a given day
q	Probability of returning to camp with food on a given day
p_1	Probability that recipient type 1 gives food back to the acquirer
p_2	Probability that recipient type 2 gives food back to the acquirer, $p_2 < p_1$
r	Number of individuals who return food with probability p_1
l	Number of k individuals who return food with probability p_1, when $n > r$
C	Exponent of the value function, assumed $0 < c < 1$
Cost	Linear cost that increases with each additional recipient

a beneficial result of pooling hunted game or gathered plant products is to reduce the daily variance in food intake among foragers, due to relatively high variance in acquisition (Sahlins 1972; Kaplan and Hill 1985; Alexander 1987; Smith 1988). There is little agreement about whether these food transfers can best be explained by reciprocal altruism (Kaplan and Hill 1985; Hames 2000; Gurven et al. 2000a), or by other models such as tolerated scrounging (Blurton Jones 1987; Vickery et al. 1991; Bliege Bird and Bird 1997) or costly signaling (Hawkes 1990; Smith and Bliege Bird 2000; Sosis 2000). The ethnographic evidence is equivocal, filled with descriptions of groups where something of value must be given for items received (e.g. Gunwinggu of Australia—Altman 1987; G/wi Bushmen of Botswana—Silberbauer 1981; Sirionó of Bolivia—Holmberg 1969) and with accounts of individuals sharing "to remain in the good graces of those who will later distribute" (e.g. Maimande of Brazil—Aspelin 1979). Other reports, however, suggest that those who produce more are unable to control the distribution of their catch, and they therefore give more because of the pressures of "demand sharing" captured by the tolerated scrounging model (e.g. Hadza of Tanzania—Hawkes et al. 2001; Pilaga of Argentina—Henry 1951; Sirionó—Holmberg 1969).

This paper supports the position that reciprocal altruism is an important explanation of within-group food transfers among foragers and forager–horticulturalists, even if tolerated scrounging or costly signaling may explain some instances of sharing. Observations that generous individuals do not receive returns according to a strict TFT mechanism are not grounds for rejecting reciprocal altruism (cf. Hawkes 1993). I investigate a general form of reciprocal altruism by considering a model with two critical features: (1) returns measured in terms of marginal value or utility rather than absolute quantities, and (2) inclusion of probabilistic degrees of cooperation. This model takes the expected actions of other individuals as extrinsic parameters that are varied to explore optimal sharing breadth and depth decisions when an acquirer returns to camp with a food resource. I first present the model, then test nine predictions generated from the model with data collected among the Hiwi, a group of foragers from neotropical Venezuela, and the Ache, a group of forager–horticulturalists from eastern Paraguay.

A model of sharing breadth and depth

An individual acquirer returns to a residential camp after a foraging bout, with a valuable food resource, F, and is faced with two sharing decisions—how much to keep for oneself (producer advantage) and how many people will receive shares of the rest? The latter refers to sharing breadth while the former refers to sharing depth (Gurven et al. 2001). The extrinsic parameters in the model are population size, N, and the prior probabilities that other individuals will return the same amount of food within some appropriate time period. These probabilities may also be interpreted as proportions of the original donations that a recipient is expected to return. A table summarizing all of the model variables to be discussed below are given in Table 1.

In modeling the above decisions, I calculate the expected return for a given sharing strategy in terms of the total value to a consumer, rather than actual amounts. I consider four levels of producer advantage, where the acquirer can (1) give the entire resource or 100%, (2) give 75%, (3) give 50%, or (4) give 25% of the acquired resource. At a given level of producer advantage, an increase in the number of recipients decreases the amount each recipient will receive because I assume that each recipient receives the same amount.

If the prior probability of return for each recipient is P, then the expected value gained by an acquirer who gives A/n to each of n recipients is $V(n) = (F-A)^c + n(PA/n)^c$, where A is the total amount given away ($F-A$ is producer priority), and c is the exponent of the value function. A power function is chosen as the value function because it is a general, flexible function, which allows for linear and non-linear increasing and decreasing value functions. For diminishing returns to scale, $0 < c < 1$, while for increasing returns to scale, $c > 1$. I assume that value is a diminishing function of amount. For any given producer priority and when $0 < c < 1$, this simple value function is maximized by sharing with as many individuals as possible (see Appendix 1a). It is also possible to derive the minimal return probability P that makes the value gained from sharing higher than the value gained from hoarding (see Appendix 1b). Therefore, when sharing is beneficial, it is best for the acquirer to share a given amount with as many people as possible, which also maximizes the total group

value. This result is also consistent with tolerated scrounging (Wilson 1997).

All individuals should gain the same marginal value from a unit of resource consumption if each distribution occurs on a different day, or after a sufficiently long time period when hunger levels return to baseline.[1] I therefore allow the possibility of simultaneous distributions by introducing the variable q, the probability that any forager returns to camp with food on a given day. If two foragers return with food on the same day, the total value gained from receiving shares from both on the same day will be less than if shares were received on separate days, assuming diminishing returns to consumption of additional portions, because $(2PA/n)^c < 2(PA/n)^c$.

The final addition to the model is to define two classes of potential recipients. Of the N individuals in the population, r individuals return food with probability p_1, while the remaining $N-r$ individuals return food with probability p_2. I let $p_1 > p_2$, and allow acquirers to display preference over who receives shares, such that all r individuals receive shares before the less reliable or less capable $N-r$ individuals.

The total expected return in value gained over an appropriate time period from receiving return shares from the n individuals who were initially given shares is:

ego will then receive a "clump" of food on the same day from those k individuals. This binomial probability that k of n individuals return to camp with food on the same day is then multiplied by the expected value from receiving the food "clump" from the k individuals and the remainder of the return food from the $n-k$ individuals. In this model, the other $n-k$ return shares are received on separate occasions. The sum of the product of these two terms over all values of k (ranging from 0 to n) gives the total return value to the acquirer of sharing A among n individuals.

If the number of recipients is greater than r, then the group of k foragers returning on the same day may be composed of individuals who return food with probability p_1, and others who return food with probability p_2. I include an additional summation in Eq. 2 that accounts for all sub-combinations of foragers within the k group that may return and share food with probabilities p_1 and p_2, on the same day. Of the k individuals returning to camp on the same day, l individuals return food with probability p_1, while $k-l$ return food with probability p_2. Of the remaining $n-k$ individuals returning food on separate days, $r-l$ return food with probability p_1, while $n-k-r+l$ return food with probability p_2. The number of sub-combinations of p_1- and p_2-type recipients that compose any cluster of k individuals will be $\min(r, k+1)$. Thus, Eq. 2

$$V(n) = (F - A)^c + \sum_{k=1}^{n} \left[\binom{n}{k} q^k (1-q)^{n-k} \times \left[\left(\frac{kA \times p_1}{n} \right)^c + (n-k) \times \left(\frac{A \times p_1}{n} \right)^c \right] \right] \quad \text{for } n \leq r \qquad (1)$$

$$V(n) = \sum_{k=1}^{n} \left[\binom{n}{k} q^k (1-q)^{n-k} \times \sum_{l=0}^{\min(k+1,r)} \frac{\binom{r}{l}\binom{n-r}{k-l}}{\binom{n}{k}} \left(\left(\frac{(l \times p_1 + (k-l) \times p_2)A}{n} \right)^c + (r-l) \times \left(\frac{A \times p_1}{n} \right)^c \right. $$
$$\left. + (n-k-r+l) \times \left(\frac{A \times p_2}{n} \right)^c \right) \right] \quad \text{for } n > r \qquad (2)$$

Because the acquirer chooses to share preferentially to the r individuals, then if $n \leq r$, only Eq. 1 is used to calculate the return value. The $(F-A)^c$ term in both Eq. 1 and 2 describes the value of food kept by the acquirer. I assume that this producer advantage is consumed in a single event. The second term in Eq. 1 gives the total return value to the acquirer of sharing A among n individuals. It gives the expected return value, averaged over possible combinations of $k=1, 2,..., n$ individuals returning back to camp with food on the same day. As discussed above, greater correlations in returns among foragers, as defined by higher values of q, will result in diminished total return value from the n recipients. If k foragers return back to camp on a given day (or alternatively if k foragers decide to share food on a given day) with probability

$$\binom{n}{k} q^k (1-q)^{n-k} \qquad (3)$$

yields the total return value to the acquirer of sharing A among n individuals consisting of both p_1- and p_2-types.

The use of summations and combinatorics complicates the derivation of an analytical solution. Instead, I illustrate the dynamics of the model with a series of figures (Fig. 3a–c), which examine $V(n)$ where $F=100$, using different values of the parameters p_1, p_2, A, and q.

When simultaneous distributions are unlikely [or when we have low inter-forager variance in acquisition (Winterhalder 1986)], as characterized by $q=0.1$, sharing is highly beneficial for the acquirer because relatively high-value returns are received on separate occasions. Even though the marginal benefits from giving decline once the acquirer shares to unlikely reciprocators (p_2), it is still worthwhile from the acquirer's perspective to continue sharing, especially if other options are even less rewarding. Furthermore, the best strategy if sharing to a few recipients is giving away a small (25%) percentage of your total, while otherwise it is best to give a larger (75%) percentage of your spoils away. This results from the fact that the total value gained by receiving shares of rela-

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[1] Individual differences in marginal value due to resource holding potential or acquisition ability are not included in this model.

tively high value is greater than the loss in value from not consuming those shares immediately after acquisition. Because return value is proportional to value given away, maximizing return value should require that sharing breadth and depth are positively correlated.

The variance–reduction benefits of sharing saturate with high values of q (Fig. 3c). However, it is evident that "give 75% away" and "give 50% away" are consistently robust strategies across a wide range of n and q. The strategy "give 100% away" is never a better strategy than less sharing and just barely better than no sharing when q is high.

If resource package size is reduced (F=10) while keeping the other variables constant, the benefits from sharing saturate relatively quickly; most of the benefits to sharing can be achieved by keeping more and by sharing to fewer individuals (Fig. 4a, b—compare with Fig. 3a, b). The extent to which package size makes a difference in sharing outcomes will depend on the location on the diminishing returns curve where most of the consumption value is reached. The shape of this curve should differ across nuclear families as a function of family size and composition because larger nuclear families with a greater number of dependent consumers relative to the number of producers will reach diminishing returns at higher levels of consumption.

I have not yet included any direct (opportunity) costs of sharing to additional individuals. The only costs included thus far are those associated with the saturation in variance–reduction benefits. However, one can imagine a linear cost function, which increases with the number of recipients. A cost is justified on the grounds that there are likely to be expenditures of time and energy spent traveling to households that might be located at some distance, gaining information about locations of potential shares, monitoring other individuals, and increased likelihood of defection. These costs should increase with the number of return shares expected. Adding a linear cost function in the value equation forces $V(n)$ to slope downward at larger n, giving interior optima for the number of recipients at each level of producer priority (Fig. 5a–c).

Implications of the model

This model determines optimal breadth and depth of sharing given the marginal valuation of resources. Marginal valuation is determined by the size and nutritional composition of resources in the diet relative to the constraints imposed by an organism's digestive system (e.g. limitations on the capacity to metabolize and store fats, protein, and carbohydrates), and by aspects of supply and demand summarized by the inter-forager and intra-forager variance in acquisition. The supply of certain foods at any point in time can affect the demand (and hence the "price") for resources at any given time. Because digestive constraints should not vary substantially among group members, this paper incorporates the latter cause of

marginal valuation, in addition to differences in marginal value caused by having larger families.[2]

The most important result of the model is that non-trivial amounts of sharing are optimal from an acquirer's perspective, assuming reciprocal altruism, even when the average probability that recipients return the resource in some short time period is less than certain. In this model, the uncertainty of return is due to both uncertainty in the food supply, and in the conditional likelihood of giving food upon acquisition, reflected respectively by low values of q and p_1 or p_2. In general, the time span over which returns are gained will be greater when q is low than when q is high. The probability of any return receipt will increase with greater n and with greater q. However, when q increases, multiple individuals are likely to return food on the same day. Finally, it may be advantageous for a reciprocal altruist, attempting to maximize the total value of return benefits, to give food away to individuals who vary in their likelihood to return the favor in kind. Even if dominant individuals coerce an acquirer to cede shares according to tolerated scrounging, this alone does not negate the possibility for reciprocal altruism with less dominant individuals.

The inclusion of producer advantage and preferential sharing to those most likely to return resources assumes some level of producer control over distribution. It can be shown that if recipients are randomly chosen with respect to p_1 and p_2, then the optimal number of recipients will decline. The tolerated scrounging assumption that hungry foragers are willing to fight harder for a contested resource, and use this leverage to extract shares from others is one that requires empirical testing. For example, if the types of high variance foods desirable for sharing are only acquired by skilled specialists, this may produce the kind of "market effect" that increases rather than decreases producer control over distribution (Nöe 1990).

Predictions

The logic and simulation results of the model allow us to make a series of predictions:

1. Nuclear families should rarely give away an entire resource package. Very rarely in the simulations was it ever advantageous to give up all immediate consumption, and rely entirely on the value of return shares of others. High depth was most beneficial only when the number of recipients was high.
2. The number of recipient nuclear families per distribution should be less than the total pool of available families whose members have as great or a greater need for access to food than members of the acquirer's

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[2] Although larger families should display higher marginal value for food because of having more mouths to feed, larger families could have smaller marginal value if additional family members are net producers. Instead, we might focus on number of dependent children, or the ratio of consumers to adult producers, as an overall indicator of marginal value.

Table 2 Summary of predictions, relevant theoretical models, and support from Hiwi and Ache analyses. *RA* Reciprocal altruism, *TS* tolerated scrounging, *CS* costly signaling

Prediction	Consistent with	Inconsistent with	Supported by Hiwi?	Supported by Ache?
1. Rarely give away entire resource package	RA, TS	CS	Mixed	Yes
2. Breadth should be restricted	RA	TS, CS	Yes	Yes
3. Positive contingency	RA	TS, CS	Yes	Yes
4. Depth and breadth vary positively with resource package size	RA, TS, CS		Yes	Yes
5. Depth and breadth positively correlated	RA, TS, CS		Yes	Yes
6. Variable food items shared with greater depth and breadth	RA, TS, CS		Yes	Yes
7. Contingency using value greater than when using amount	RA	TS, CS	Mixed	Yes
8. High producers share with greater depth and breadth	RA, TS, CS		Mixed	Yes
9. Large families should share with less depth and breadth	RA, TS	CS	Mixed	Mixed

family. As returns to sharing diminish with the number of recipients, and with increasing costs, sharing breadth should include a small or intermediate number of individuals.

3. Nuclear families should preferentially share with other families who are likely to reciprocate. There should be a positive "contingency" between giving and receiving. The return benefits to sharing require positive values of return probabilities, p_1 and p_2.

4. The percentage of a food item given away to members of other families for any given distribution (depth) should vary positively with the original size of the resource. The number of recipients per distribution (breadth) should also vary positively with the size of the resource. While sharing may be favorable for both small and large resources, the analysis shows that greater marginal returns can be achieved by higher depth and breadth for large items.

5. When the number of recipients is low, little should be given away, while a greater proportion of the resource should be given away when the number of recipients is high. Sharing depth and breadth should therefore be positively correlated. The simulations reveal that when breadth is low, greater returns are realized with lower sharing depth, while large breadth requires higher depth to reap the most gains. This will be especially true with larger resource packages.

6. Difficult-to-acquire resources, with variable acquisition success exemplified by low values of q, should be shared with greater breadth and depth, controlling for resource package size. When q is low, benefits to sharing are greatest, and saturate at the slowest rate with increased breadth of recipients.

7. If food value is a more salient fitness currency than quantity, then contingency of receiving based upon giving should be greater when exchange is measured in terms of value rather than quantity. This prediction follows from the assumption in the model that value diminishes with greater consumption, and the logic that value received back from recipients is a more salient currency than absolute quantity.

8. Nuclear families with higher production are expected to give away more food, and possibly to a greater number of families, than families with low production. While high producers may display lower marginal value for additional resources, giving is also less costly for them, and so the loss of immediate value from foregoing complete consumption is less, as is the cost of only partial receipt in the future.

9. Larger nuclear families with greater dependency should give less, controlling for family food production. Families with a greater ratio of consumers to producers should display a greater value for immediate consumption, for the same reasons stated in prediction 8 regarding families with low production. To the extent that high dependency families also discount future benefits, less sharing will be expected.

Table 2 summarizes the nine predictions and links these to the three models of reciprocal altruism, tolerated scrounging, and costly signaling. Only predictions 2, 3, and 7 are unique to reciprocal altruism. Predictions 4–6 and 8 are also consistent with both tolerated scrounging and costly signaling. Predictions 1 and 9 are consistent with tolerated scrounging but inconsistent with costly signaling. Predictions 7–9 are not requirements of reciprocal altruism per se, but are explorations of contingency and balance using the more realistic currency of value rather than quantity.

All analyses of Hiwi and Ache sharing behavior are done at the level of nuclear families rather than individuals. Depth therefore describes percentages given to other families, and breadth refers to the number of family recipients. Food transfers to specific individuals are often difficult to monitor, especially because acquirers understand that primary distributions to specific individuals in other families are usually followed by subsequent distributions within those families. In both populations, food transferred provided only a rough estimate of who actually consumed the food, and intra-family sharing of all resources was ubiquitous. The logic of marginal valuation applies equally well to families as is does to individuals, although families will differ in the extent to which food is valued as a function of the number and ability of producers and consumers.

Methods

Below I present brief ethnographic descriptions of the Hiwi and Ache populations, and summarize the methods used for collecting the data on food transfers.

The Hiwi of Venezuela

The Hiwi are a group of foragers that live in the llanos, or neo-tropical savannas, of southwestern Venezuela (see Hurtado and Hill 1990; Hurtado et al. 1992 for background on diet, seasonality, sexual division of labor, demography, fertility, and child care). In the 1980s, roughly 95% of the Hiwi diet consisted of wild foods, making the Hiwi full-time hunter–gatherers during the time of study (Hurtado and Hill 1990). Game and fish accounted for roughly 60% of the diet by weight and 68% of the total calories consumed, whereas plant resources accounted for roughly 35% of the diet by weight and 27% of the total calories consumed.

A generalized pattern of men hunting and women gathering describes the Hiwi division of labor, although men also gather mangoes during the late dry season. Men hunt solitarily all year-round and also in pairs when traveling by canoe to hunting sites. Women walk to foraging areas mainly in and along gallery forests that are close to the permanent settlement. Men and women also forage together in husband–wife pairs 19% of the time during the root season and 56% of the time otherwise (Hurtado and Hill 1992). These foraging events usually involve canoe travel, where women help navigate canoes and spot game.

The study population consists of 106 Hiwi foragers organized into 37 nuclear families in 14 dwellings spaced about 100 m along a levee of the Capanaparo River. It should be emphasized that although the Hiwi diet consists almost entirely of wild foods, they live in a large permanent settlement much of the year. On about 85% of all person–days monitored, the Hiwi slept in the main village, whereas they slept in temporary camps on only 8% of all person–days (Hurtado and Hill 1990). Remaining sample days were spent visiting other settlements. Data were collected with Hiwi foragers at the Mahenemuthu settlement in Venezuela by A.M. Hurtado and K. Hill. All data were collected during the 1987–1988 field season from December to February and in parts of the wet season from April to May.

On sample days, data were collected on every fifth resource brought back to camp amongst a group of families, which due to time constraints were biased towards sampling acquirers that lived relatively close to the anthropologists. The resource type, original package size, acquirer, weights of all pieces, and names of all recipients were recorded. Most weights were measured to the nearest 0.1 kg with either a 10-kg or 20-kg spring scale, although some weights such as a group of mangoes were estimated by visual inspection. Each observation of the people who received a share of a particular resource item was called an event. The first distribution of a focal resource was called a primary sharing event. This distribution precedes any consumption or cooking. The data include 112 primary sharing events that represent 1,190.3 kg of food acquisition. There were 447 food transfers during those events, comprising 846.0 kg of food given to someone other than the acquirer. When individuals redistributed portions received from primary distributions to still other recipients, this represented a secondary sharing event. Secondary sharing events were only sampled occasionally and represent only 29 out of the total 141 recorded sharing events. Descriptions and analyses of Hiwi food sharing patterns are given in Gurven et al. (2000a).

The Ache of Paraguay

The Northern Ache of eastern Paraguay were full-time neo-tropical hunter–gatherers occupying a 15,000-km^2 area of eastern Paraguay up until the time of peaceful contact in the mid-1970s (see Hill and Hurtado 1996 for a detailed ethnography and life history of pre- and post-contact Ache). Even 20 years after the establishment of several permanent mission settlements, the Ache continue to spend about 20% of their time in the forest on extended mixed-sex group treks, ranging in length from a few days to several weeks (Gurven et al. 2002). For less than 20 years, the Ache have been cultivating small fields of sweet manioc, beans, peanuts, corn, sweet potato, and sugar cane. They also raise chickens, pigs, and several cows and horses, as well as "pet" monkeys, coatis, and peccaries. Wage labor assisting ranchers and cultivating Paraguayan fields is not uncommon, and provides the bulk of the income that the Ache use to purchase market foods such as yerba mate tea, salt, sugar, rolls, clothes, and pasta. Analysis of production data indicate that the bulk of the calories consumed on the settlement comes from cultigens (80%), whereas 9% comes from store-bought foods, and only about 11% comes from meat (wild and domesticated).

Food sharing data were collected by the author and W. Allen-Arave in the reservation of Arroyo Bandera (n=121 individuals, 23 nuclear family-based households) over 55 sample days between February and May 1998. A total of 380 complete food distributions were sampled using a combination of focal-household cluster observations (78% of all distributions), focal-resource sampling (10%), and interviews (12%). Focal-household cluster observations were 3-h observation blocks of all food distributions, consumption, and production of all members of two or three households. Each household was sampled in this manner for an average of 56 h, giving a total of 1,294 house–hours of observation for all 23 households in Arroyo Bandera. For each food distribution, we recorded the donor, the original acquirer (if different), all recipients, estimates of 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. Descriptions and analyses of Ache food sharing are given in Kaplan and Hill (1985), Gurven et al. (2001), and Gurven et al. (2002).

Parameter estimates

Although marginal valuation, and increasing costs of sharing with larger numbers of people have not been explicitly measured for any group, values for q, F, and N are attainable for most studied populations. Among the Hiwi, N=37 potential families, and N=22 potential families for the Ache. Among the Hiwi, on average, meat items were 12.8 kg (SD=14.0), fish packages were 4.9 kg (SD=7.5), and other items were 10.7 kg (SD=12.4). Among the Ache, on average, cultigens were 3.0 kg (SD=7.3), store bought foods 1.3 kg (SD=1.0), forest foods 4.3 kg (SD=4.1). The probability that a hunter returns to camp successful with a kill is about 35% (q=0.35) for the Hiwi, and 60% (q=0.6) for the Ache.[3] Thus, the Hiwi can expect to bring back foraged food at least once with 72% probability every 3 days, or with 95% probability every week. The Ache will acquire foraged food at least once with 94% probability in 3 days, and almost certainly within a week (Table 3). Even though

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[3] These values of q are conditional upon a foraging event. The probability that individuals go foraging on a given day at the Ache reservation and the Hiwi settlement varies from 0.1 to 0.4.

Table 3 Table 3 Probability that a forager returns to camp with a food item at least once in 1, 3, 7, and 30 days, assuming daily probability of returning to camp with a food item, q={0.1, 0.3, 0.5, 0.7, 0.9}

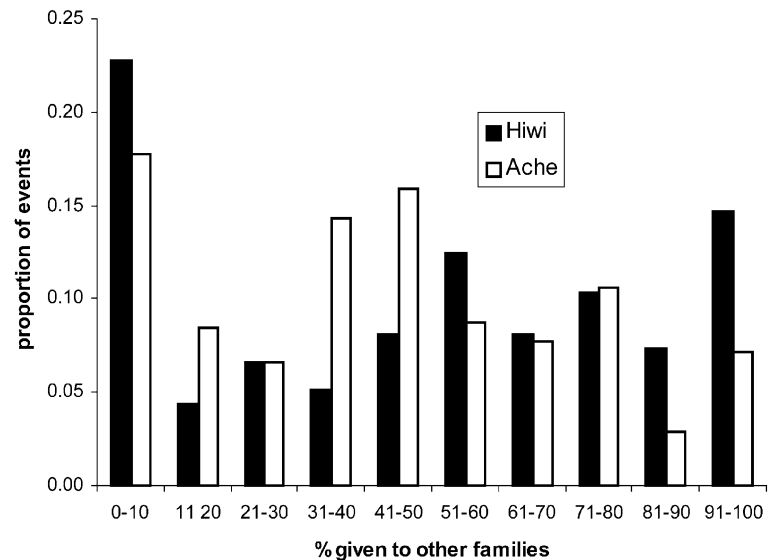| q	1 Day	3 Days	7 Days	30 Days
0.1	0.10	0.27	0.52	0.96
0.3	0.30	0.66	0.92	1.00
0.5	0.50	0.88	0.99	1.00
0.7	0.70	0.97	1.00	1.00
0.9	0.90	1.00	1.00	1.00

time discounting of future benefits was not explicitly incorporated into the breadth–depth model, Table 3 shows that under a wide range of intermediate q values, individuals will have an opportunity to transfer food brought back to camp within the span of a week. Estimates of q for non-foraged foods are not available, but are likely to be high. For example, most Ache own fields, and so the availability of farm foods in the village is dependent upon the frequency of prior harvest, because the probability of successful acquisition will be close to 100%.

Results

Prediction 1

A first test of the model is to explore the extent to which anyone gave away entire food items. Figure 1 presents a frequency distribution of the percentages of specific resource items given to members of other nuclear families. More than 80% was given away in 21% of all Hiwi and 10% of all Ache sampled events. A chi-squared test of independence reveals, however, that the frequency distribution of percentages given away are not random ($\chi^2=37.09$, $P<0.001$ for Hiwi; $\chi^2=72.63$, $P<0.0001$ for Ache, $df=9$). Of the 18 Hiwi events where everything was given away, the acquirer was male in 10 of these events, and the mean age of the acquirer was 42 years old. Of the 21 Ache events where everything was given away, the acquirer was male in 13, and on average was 32 years old. These items given completely away had a mean package size of 13.8 kg for the Hiwi, and 5.7 kg for the Ache (about 68.3% and 90.0% larger than the mean for less widely shared resources among Hiwi and Ache, respectively) and were more likely to be meat items (31.6% vs 25.4% for Hiwi; 47.6% vs 23.3% for Ache). The examples of widespread giving are consistent with costly signaling, although that model is usually applied only to males who stand to gain mating benefits from costly displays. However, women (and men) may signal a costly intent to engage in cooperative social relations, rather than phenotypic quality. Such signaling of intent is usually embedded within a system of reciprocal altruism (Gurven et al. 2000b).

Prediction 2

Although the model predicts a wide range of possible recipients as the optimum under different circumstances, incorporating monitoring and travel costs for the Hiwi should give us an intermediate optimum that is less than the total number of potential recipients (36 nuclear families for the Hiwi, 22 for the Ache). A frequency distribution of the number of recipient families reveals that most events saw only several recipients (Fig. 2). In fact, there were less than four recipient families in about three-fourths of all Hiwi and Ache events. The average number of recipient families over all events was 2.6 for the Hiwi and 1.9 for the Ache. It seems likely, however, that this sharing breadth is smaller than would be expected from tolerated scrounging, because travel and information costs are unlikely to be very high (mean distance between nuclear families =32 m for Hiwi, 108 m for Ache). Events where the acquired resource was large or high variance (low q) tended to witness higher average numbers of recipients, consistent with tolerated scrounging, costly signaling, and reciprocal altruism (Gurven et al. 2000a).

Prediction 3

Although minimal probabilities of receiving return benefits in order to make sharing a favorable strategy have not been explicitly estimated, they should at least be significantly positive. Gurven et al. (2000a) introduced a "contingency" measure, which attempts to capture the conditionality of giving upon prior, and presumably expected future, receiving. One way of measuring contingency is to calculate the standardized regression coeffi-
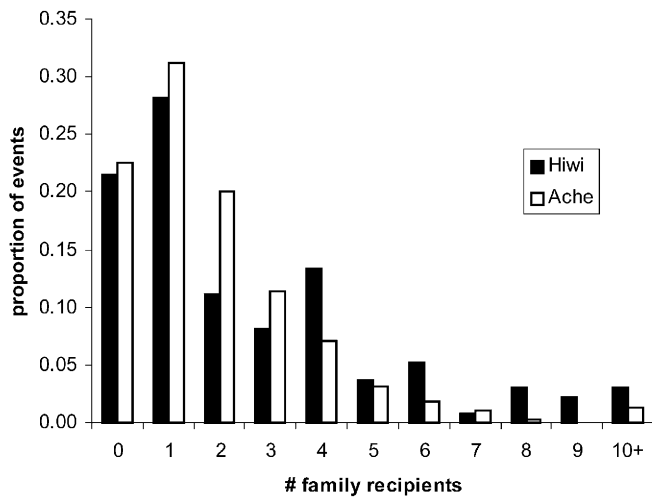
Fig. 1 Frequency distribution of the percentage of food given to other nuclear families for Hiwi ($n=135$) and Ache ($n=378$)

Fig. 2 Frequency distribution of the number of nuclear family recipients per event for Hiwi (*n*=135) and Ache (*n*=378)

cient of the total kilograms or percentage of family A's production given to family B on the total kilograms or percentage of family B's production given to family A, for all pairs of families. Because each pair of families contributes two perfectly correlated data points, only half of the sample is used for the analyses.[4] A control variable for the percentage of food a donor family gave away to all others was included in all analyses in Table 4, to account for the lack of independence between data points. The estimates for Hiwi exchanges of meat, fish, other foods such as honey, roots, mangoes, and all food resources are given in Table 4. The kilogram currency (column 1 of Table 4) may introduce bias in the Hiwi contingency estimate because of the non-random sampling of events in this case. I standardize the kilogram currency by dividing the kilograms A gave to B by the total kilograms produced by A, yielding the "percentage" currency given in column 2 of Table 4. All estimates except for those in the "other" category are statistically significant at the 0.05 level. The evidence suggests a range of 0.20–0.60 for meat and fish resources and an average of 0.20–0.30 for all foods returned to initial donors.

For the Ache, coefficients are given for the exchange of foraged foods, cultigens, store bought items, and all food resources. Contingency is greatest for store bought foods, intermediate for cultigens, and smallest for foraged items. All contingency estimates are statistically significant at the 0.05 level except for the exchange of foraged foods when kilograms are used as the currency of exchange. The standardized correlations using percentages are mostly of greater magnitude than those using kilograms. The contingency correlations hover between 0.30 and 0.40, with foraged foods averaging less (0.09) and store bought foods more (0.40–0.50).

A strong test of contingency must show that the conditionality of giving is dependent upon receiving, and not upon other characteristics of social relationships. Biological kinship and geographical proximity between families are two important features that define social relations among individuals. Biological kinship between families A and B is measured as the closest coefficient of genetic relatedness between any member of A and any member of B. Geographical proximity is measured as the distance in meters between residence locations of A and B. Table 4 also gives contingency estimates, controlling for the effects of biological kinship and geographical proximity among families (Table 4, columns 4 and 5). The qualitative conclusions made from examining the univariate results remain the same with the multivariate analysis. However, the quantitative estimates are somewhat reduced when the partial effects of kinship and proximity are included in the analysis.

Prediction 4

Large resources characterized by medium to high diminishing returns in value with each additional amount consumed should be transferred outside the nuclear family more extensively than small resources, according to both reciprocal altruism and tolerated scrounging. Thus, sharing depth and breadth should be greater, not only because hungry foragers are more likely to fight harder to obtain shares of larger resources, but because these same conditions maximize the expected return to an acquirer given the distribution of prior probabilities of returning resources among potential recipients.

Regressions of package size on the percentage given to other families per event and on the number of recipients per event are statistically significant in the predicted directions for both Hiwi and Ache. On average, each 1-kg increase in the package size of a resource is associated with a 1.1% increase in depth among the Hiwi and 0.7% increase among the Ache, and an additional 0.2 Hiwi and Ache recipient families (Table 5, results 4a, b).

Prediction 5

In the simulations, there was a crossover point where the best strategy shifted from "give 25% away" for low *n* to "give 75% away" at higher *n*, over a wide range of *q*. Thus, we might expect that more recipients should receive shares when more is given outside the nuclear family than when less is given away. This is not a trivial prediction, because any fixed percentage given away may be distributed among few or many nuclear families.

A regression of percentages given away on the number of recipient families for those events reveals that about 20% more is given away on average for each additional Hiwi recipient nuclear family, and 7% to each additional Ache family (Table 5, result 5a). Even when the size (in kg) of the resource is controlled in a multiple regression,

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[4] For each pair of correlated data points, I randomly chose one to use in the analysis and discarded the other.

Table 4 Contingency correlations for Hiwi and Ache. Contingency refers to the amount or percentage of family A's food production given to family B correlated with the amount or percentage of family B's food production given to family A. Amounts are measured in kilograms, percentages refer to the percentage by weight of food shared with other specific families, and value is estimated as the sum of the square root weights given to specific other families. Columns 4–6 provide contingency estimates which control for biological kinship and geographical proximity among families. All analyses also control for the percentage of the resource type given to all others

Hiwi and Ache contingency correlations							Controlling kinship and proximity					
Resource type	kg–kg	P	%–%	P	value–value	P	kg–kg	P	%–%	P	value–value	P
Hiwi												
Meat	0.648	**	0.398	**	0.407	*	0.690	**	0.369	*	0.482	*
Fish	0.171	-	0.489	**	0.327	*	0.162	–	0.498	**	0.329	*
Other	0.085	-	0.143	-	0.075	-	0.078	-	0.132	-	0.072	-
All	0.284	***	0.226	**	0.195	**	0.293	***	0.205	**	0.203	**
Ache												
Forest	0.086	-	0.093	*	0.320	***	0.043	-	0.020	-	0.226	**
Cultigens	0.283	***	0.347	***	0.464	***	0.206	**	0.261	***	0.334	***
Store bought	0.537	***	0.422	***	0.459	***	0.476	***	0.332	***	0.339	***
All	0.277	***	0.365	***	0.651	***	0.207	***	0.253	***	0.531	***

*** $P<0.0001$, ** $P<0.001$, * $P<0.05$

Table 5 Results of hypothesis testing for breadth–depth model

	Hiwi							Ache			
Hypothesis	Y[a]	X[a]	Predicted direction	Parameter estimate	P-value	R^2	df	Parameter estimate	P-value	R^2	df
4 (a)	%give	Package	+	1.117	<0.0001	0.14	133	0.740	<0.0001	0.04	373
4 (b)	#recips	Package	+	0.163	<0.0001	0.48	133	0.197	<0.0001	0.47	373
5 (a)	%give	#recips	+	20.408	<0.0001	0.38	133	6.674	<0.0001	0.28	373
5 (b)	%give	#recips	+	13.400	<0.0001	0.62	132	9.258	<0.0001	0.33	372
	-	Package	+	1.052	<0.0001	-	-	1.083	<0.0001	-	-
6 (a)	%give	VI	+	0.499	0.009	0.05	133	0.521	<0.0001	0.09	359
6 (b)	%give	VI	+	0.365	0.043	0.17	132	0.477	<0.0001	0.11	358
	-	Package	+	1.034	<0.0001	-	-	0.652	<0.001	-	-
6 (c)	#recips	VI	+	0.029	0.057	0.03	133	0.037	<0.0001	0.08	359
6 (d)	#recips	VI	+	0.009	0.455	0.48	132	0.024	<0.0001	0.43	361
	-	Package	+	0.161	<0.0001	-	-	0.179	<0.0001	-	-
6 (e)	VI	Package	+	0.208	0.070	0.03	133	0.346	<0.005	0.02	362
8 and 9 (a)	%give	Totprod	+	0.087	0.306	0.23	28	0.265	0.018	0.24	21
	-	C/P	–	−18.307	<0.0001	-	-	−6.682	0.112	-	-
8 and 9 (b)	#NFs	Totprod	+	0.079	<0.0001	0.54	28	0.085	<0.0001	0.48	21
	-	C/P	–	−1.197	0.276	-	-	−0.005	0.995	-	-

[a] Variables: *%give1* the percent given away to members of other families for each event, *%give2* the percent of total production given away over sample period, *package* weight (kg) of an acquired resource, *#recips* the number of recipients (not including one's own family) that receive a share for each event, *#NFs* number of nuclear family recipients that received any food during the sample period from focal donor family, *VI* variance index, an overall measure of acquisition variance, *C/P* ratio of number of consumers (>17 years old) to number of producers in a nuclear family, *totprod* total food production in kilograms over the sample period

the significant effect of number of recipient nuclear families still remains (Table 5, result 5b–13% greater depth for Hiwi, 9% for Ache).

Prediction 6

Gurven et al. (2000a) estimated production variance using a variance index (VI) measure. *VI* is a composite of three separate measures: $VI=(V_e+V_g)V_a$, where V_e is the variance in encounter rates per person–hour spent searching, V_g is the variance in energy obtained per pursuit, and V_a is the degree of asynchronicity of acquisition, or the opposite of "inter-forager correlation" (Winterhalder 1986).

Each resource in the sample was ranked on all three variance measures, each ranging from 0 for lowest to 4 for highest. This ranking was done by Kim Hill and the author based on foraging experiences and without prior knowledge of the extent of sharing of each resource. The *VI* measure was structured so that sharing provides no variance reduction benefits when there is complete synchronicity in acquisition ($V_a=0$), regardless of the level of variance in the other measures ($0 \leq VI \leq 32$).

Resources with higher *VI* scores are transferred more outside the family (Table 5, result 6a), even after controlling for resource package size (Table 5, result 6b). This result is consistent with the prediction for sharing depth. However, the association between *VI* and the

number of recipients per event appears to be an artifact of package size for the Hiwi, but not for the Ache (Table 5, results 6c, d). Thus, it does not appear that higher variance resources are always shared to more individuals independent of the fact that larger resources have higher *VI* scores (Table 5, result 6e).

Prediction 7

Sharing imbalances, when measured using differences in absolute amounts transferred among a pair of nuclear families, may diminish when measured using differences in the total value of food exchanged. Column 3 of Table 4 shows the contingency estimates obtained when using a square-root transformation for each food transfer. This non-linear scaling of amount is an estimate of value that meets the diminishing returns assumption. The total value given by A to B is calculated as the summed valued transfers given by A to B. As in the analysis of contingency using currencies of kilograms or percentages, Table 4 includes both univariate estimates of value-based contingency (Table 4, column 3), and partial estimates, which control for the effects of kinship and geographical proximity between families (Table 4, column 6). Among the Hiwi, only the contingency estimate for fish is greater when measured in value rather than amount (0.33 vs 0.17; partial estimates: 0.33 vs 0.16). Among the Ache, the standardized estimates using value are greater than those using kilograms for forest items (0.32 vs 0.09; partial: 0.23 vs 0.04), cultigens (0.46 vs 0.28; partial: 0.33 vs 0.21), and for all food items (0.65 vs 0.28; partial: 0.53 vs 0.21). Contingency for store bought foods was strongest when calculated using kilograms, although still significantly high when calculated using value.

Predictions 8 and 9

For each family A, I calculate (1) the total amount acquired over the entire sample period, (2) the ratio of the number of consumers to the number of producers in family A, where consumers are defined as those less than 17 years old, (3) the percentage of all food given to other families over the entire sample period, and (4) the total number of families who received some food from family A over the sample period. The set of regressions includes all families who acquired more than 10 kg over the entire sample period.

The results in Table 5 show that breadth and depth outcomes among the Ache are affected by total food production (standardized parameter estimates: 0.59, 0.69), but not by donor family need. Ache consumer–producer ratios are positively correlated with total food production ($r=0.56$, $P=0.005$), and so may be a poor measure of need. Per capita family production does not change with increases in family size (standardized beta=0.06, $P=0.77$, $df=21$), which suggests that families adjust their work effort to compensate for life cycle stage and fertility.

Nonetheless, both depth and breadth are strong positive functions of per capita production (standardized beta =0.71, $P<0.0001$; standardized beta =0.61, $P<0.002$).

Breadth among the Hiwi is a positive function of total production, while depth varies only as a negative function of donor family need, as measured by the consumer–producer ratio (standardized parameter estimates: 0.73 for breadth, −0.46 for depth). Controlling for production, families with relatively larger dependency are giving a smaller percentage away, but to the same number of families, as those with low dependency. Controlling for dependency, families with greater food production give the same percentage away, but distribute the shares to more families.

Discussion

The Hiwi and Ache data support the predictions of the model that intermediate levels of producer advantage should exist, that the average number of recipients is much smaller than the total number available, that large and high variance resource items are shared with greater breadth and depth than small and low variance items, and that contingency between giving and receiving exists among pairs of families. Although I predicted that contingency would be stronger when measured in terms of value transfer rather than quantity, this result was only consistently supported by the Ache data. Several of the results reported in this paper are not new and may be explained by other models (Table 2), but the formal approach taken in this paper allows us to derive aspects of sharing breadth and depth as a function of several variables—the probabilities that others return food, the package size of resources, acquisition variance, and group size. To date, no prior model, including previous specifications of reciprocal altruism, have attempted to explain variation in both sharing depth and breadth. The predicted results derive from the assumptions of diminishing marginal valuation of food consumption, moderate levels of acquisition variance across individuals, and preferential sharing—characteristics that generalize to many forager and forager–horticultural populations (Gurven 2004).

The implication of this paper is that reciprocal altruism is important despite the simultaneous occurrence of other avenues of sharing, and therefore cannot be dismissed from future discussions of food transfers. Although probabilities of receiving food conditional upon giving food may be positive across certain pairs of nuclear families, these actual probabilities may be significantly lower than the maximum 1.0, as a result of tolerated scrounging, subtle cheating, kin biases, and bargaining (Gurven et al. 2000a), while measured probabilities will also suffer from substantial sample variance. Reciprocal altruism is relevant as long as the probabilities are above the minimal threshold that makes continued sharing beneficial. Contingency estimates for the Hiwi and Ache are significant, even when we control for kinship and proximity, which means that contingency is not a

byproduct of symmetrical social relations or kin-biased transfers. It is important to mention here that positive probabilities of receiving return shares are possible with tolerated scrounging, but only in very small, highly structured groups, where individuals routinely play both the roles of producer and receiver. Under these restrictive conditions, it may be very difficult to disentangle reciprocal altruism from a form of tolerated scrounging with punishment (Gurven 2000). The turn-taking in production roles means we should more aptly refer to this kind of scrounging as reciprocal tolerated scrounging. Strict tolerated scrounging would allow individuals to stop producing food but still maintain access to the foods of others. If constant food production by able-bodied individuals is locally enforced, then tolerated scrounging is still better thought of as a form of reciprocal altruism because receiving is contingent upon food production and work effort, rather than giving.

The three unique predictions of reciprocal altruism (predictions 2, 3, and 7; Table 2) were supported with the Ache and Hiwi data. The results of these three test predictions are inconsistent with both tolerated scrounging and costly signaling. However, one ambiguous result is that contingency among the Hiwi, when measured in terms of value, was greater than when measured in terms of amount only for fish transfers. One possibility is that the arbitrary use of the same value function for all transfers may not be appropriate in all contexts. The true value of a share receipt must consider the quantities of food already available to a family at the time of receipt. Unfortunately, such detailed data do not exist for the Hiwi, Ache, or any other population. Foods also differ in their capacity for storage, and therefore in the ways that quantity relates to value. Large quantities of meat and fish are rarely stored for more than a few days, even though the technology to do so exists among the Hiwi and Ache. Agricultural foods among the Ache are sometimes stored, although they may be stored in the ground (e.g. sweet manioc) rather than in the house. Large harvests of fruits and some cultigens suggest an inclination to share when acquirers choose to bring a large resource package back to the village that exceeds the immediate consumption value of household members. Another possibility is that among the Hiwi, those who gave a greater total quantity of food to specific others were more likely to give to these others more frequently. Reducing imbalance, and thereby increasing contingency, requires that those who received more than they gave should have given more frequently to those who gave more to them. Indeed, for transfers of all foods, only 7% of the pairwise family data points saw a decrease in quantity imbalance in this manner, whereas 20% of the data points for the Ache were consistent with reducing quantity imbalance.

The mixed support for predictions 8 and 9 may have been partly an artifact of the small samples used in these analyses, where the number of data points was equal to the number of families. Multivariate analyses at the level of single distribution events have shown that high producers share with greater depth, and that larger families with greater dependency share with less depth and breadth, among both the Hiwi (Gurven et al. 2000a) and Ache (Gurven et al. 2001, 2002).

There are other reasons not explored in this paper but dealt with at length in others (e.g. Gurven et al. 2000a; Gurven et al. 2001) for why individuals might give food away to others. Individuals who payback resources with a low probability may still receive shares if they are close kin to the donor, if giving has high signal value that yields an appropriate return (but not necessarily from those specific recipients), if the low probability of return is due to poor production ability rather than an unwillingness to produce food or share[5], or if these individuals are likely to return other utility-enhancing resources or commodities through trade. Family, extended kin, and other preferential transfer biases to specific individuals may represent other avenues for fitness increase than from direct reciprocal altruism with a few limited partners.

This paper has argued that the reciprocal altruism framework can explain much variation in food transfer patterns among the Hiwi and Ache, even though restrictive TFT models may be poor analogues for individuals' actual cooperative behavior. Reciprocation may be partial, returns may occur after a delay and hence after additional food offerings, information about others' production may be incomplete, and partners may display "acceptable" reasons for not reciprocating enough (e.g. brief bout of sickness, illness, large family). One possibility for the maintenance of unequal sharing relations is that high producers either gain more from sharing than low producers or that they pay lower costs than low producers (Gurven et al. 2000b; Smith and Bliege Bird 2000), again suggesting that the marginal value of food is critical to understanding food transfer decisions. Research in economic bargaining theory suggests that there is no reason to expect equal quantities or even values of resources to be exchanged between interested parties. Equal sharing as envisioned by TFT is only likely if the bargaining power of all players is identical. Given differences in production abilities and the availability of other economic options across individuals, a bargain or "cooperation" event can still occur even if the terms of an agreement favor one party more than the other. All that is necessary for a bargain to occur is for the benefits to both parties resulting from the bargain to be greater than those received by no bargain. The bargain is then how much of an individual's production is given to another in exchange for a certain expected amount of the other's future production. The magnitude and direction of resource flow can only be predicted by understanding the context of that distribution.

Costly signaling is a relatively unexplored explanation for extensive sharing where giving acts as an honest

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[5] The amount one can expect to receive from an individual is a function of both her willingness to share and the amount of food she produces. Individuals less willing to share may still receive food from others if their production is above average. Likewise, those who produce less, but give proportionally more, may also receive food.

signal of production ability (Smith and Bliege Bird 2000; Gurven et al. 2000b). The signal may be honest in the Zahavian sense because only skilled acquirers (especially ones looking for mates or seeking social attention) can give in great depth and breadth without experiencing much difficulty in acquiring more food. Widespread sharing can also signal a willingness to cooperate (and not defect) (Gurven et al. 2000b), which can be honest if individuals share when it is economically unwise in the short-term. "Showing-off" (Hawkes 1990, 1993) may be best understood from this signaling perspective. Of the nine predictions tested in this paper, the results of three of them are inconsistent with costly signaling (Table 2). There is some support for costly signaling from the test of the first prediction, where a non-trivial amount of sharing entire resource packages was evident among the Hiwi, and to some extent, the Ache. However, these instances of widespread giving were not confined to males, the usual category of individuals expected to engage in costly displays. Confirmation of sharing as costly signaling will entail an exploration of non-foraging social benefits, which may or may not require any contingency between giving and receiving among pairs of individuals or nuclear families.

It is important to realize that the breadth–depth model is not dynamic (cf. Skyrms and Pemantle 2000), but can serve as a springboard for the construction of more realistic models. The model gives the optimal sharing breadth (assuming depth is given) or sharing depth (assuming breadth is given) for an acquirer only under fixed socioecological conditions. If, however, the probabilities of return are not extrinsic to the model, but interact with the acquirer's sharing decisions, then sharing behavior could change over time. The model ignores the prior history that may have caused those probabilities and only examines the probabilities at the time of a single distribution. One interpretation is that these probabilities are "stable", and represent the weighted history of past sharing. However, it is not clear without explicit modeling whether these probabilities or many others would indeed be stable. The interactions between one's own sharing decisions and those of others over time is an important issue that merits future attention.

Conclusion

Existing models of food transfers (e.g. Winterhalder 1986; Blurton Jones 1987; Hawkes 1990; Smith and Boyd 1990) have shown how pooling resources can be beneficial given certain characteristics of the local ecology and the production capabilities of individuals. Sharing of high variance foods that come in large packages among only a handful of active foragers at a given point in time yields, on average, large risk-reduction benefits to consumption, especially among members of long-lived social species. Although food transfers may benefit many individuals in a population, this fact alone does not determine which individuals will be the ones to actively produce food and

share widely [who actually produces food might resemble a game of chicken, rather than a prisoner's dilemma (Boone 1992; Hawkes 1992)]. The fact that not all group members benefit equally from sharing networks has led some to question the relevance of reciprocal altruism for explaining transfers (Hawkes 1993; Bleige Bird 1999).

We are in a position to construct and ultimately test better models only with an understanding of the kinds of data we can collect in field settings. It is still too early to reject egoistic models in favor of alternative models, such as trait–group selection (e.g. Wilson 1997). For example, trade reciprocity was proposed by Kaplan and Hill (1985) as a plausible model of food transfers but has not yet been adequately tested in any traditional population! However, trade often does not involve time delays, and may not reduce acquisition variance. There is a great need for workable marginal valuation-based models, and models that allow for negotiation within a given "bargaining zone" (Nöe et al. 1991). Comprehensive models that deal with extrinsic resource characteristics (diminishing returns, constant returns, or increasing returns to scale, package size, macronutrient composition, and acquisition variance) and intrinsic socio-ecological features (work effort decisions, sharing behaviors of others) will help us better understand variation in sharing behavior across and within groups.

Appendix 1a

For a fixed producer priority level at $F-A$, it will be more beneficial to share to an additional individual when $V(n)>V(n-1)$.

$$(F-A)^c + n\left(\frac{PA}{n}\right)^c > (F-A)^c + (n-1)\left(\frac{PA}{n-1}\right)^c \quad (4)$$

$$\left(\frac{n}{n-1}\right)^{1-c} > 1 \quad (5)$$

The inequality (Eq. 5) is true when $c<1$. Therefore it will always be better to increase sharing breadth when the value function is characterized by a diminishing returns curve.

Appendix 1b

It will be advantageous for an acquirer to share with n individuals, and not hoard, when $V(n)>V(0)$. We can

a)   r=10, (p1=0.8) (p2=0.2), q=0.1, c=0.5

b)   r=10 (p1=0.8) (p2=0.2), q=0.5, c=0.5

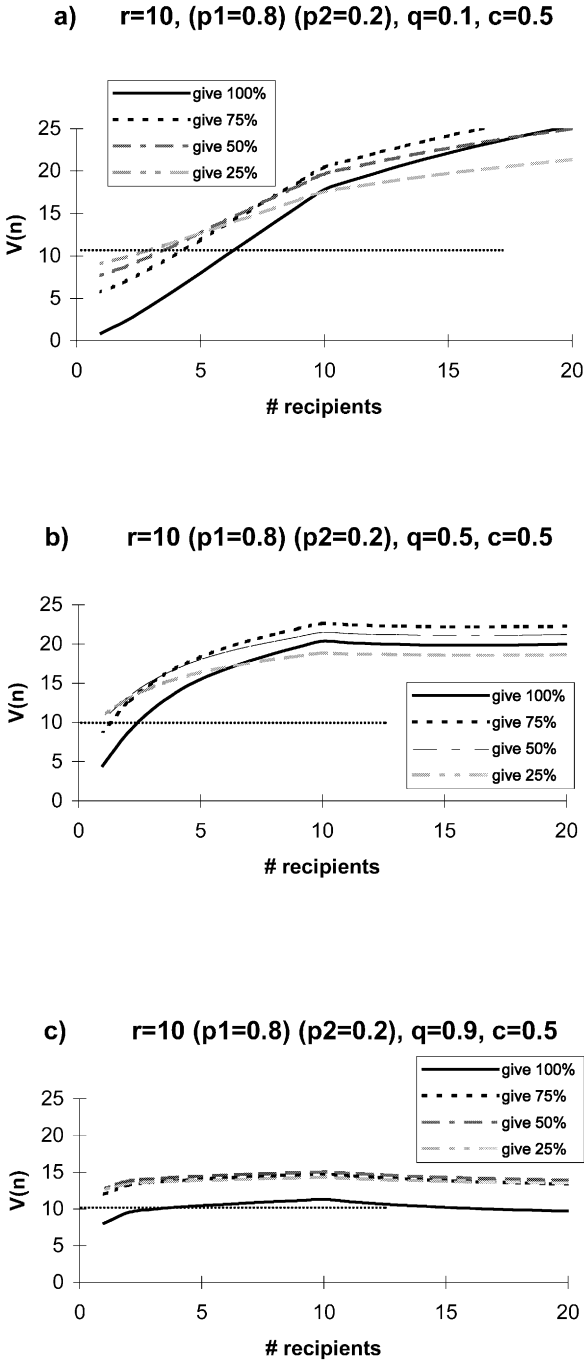c)   r=10 (p1=0.8) (p2=0.2), q=0.9, c=0.5

Fig. 3a–c Simulations of the sharing breadth–depth model. Resource package size F=100. *Horizontal line* represents the expected value if none is given away. $V(n)$ refers to the expected value an acquirer will receive over a relevant time period from sharing 25%, 50%, 75%, and 100% of a resource. Ten individuals return food with a probability p_1=0.8, and ten with probability p_2=0.2. The variable q describes the probability that two foragers return food to an acquirer on the same day, and varies in **a** q=0.1, **b** q=0.5, and **c** q=0.9
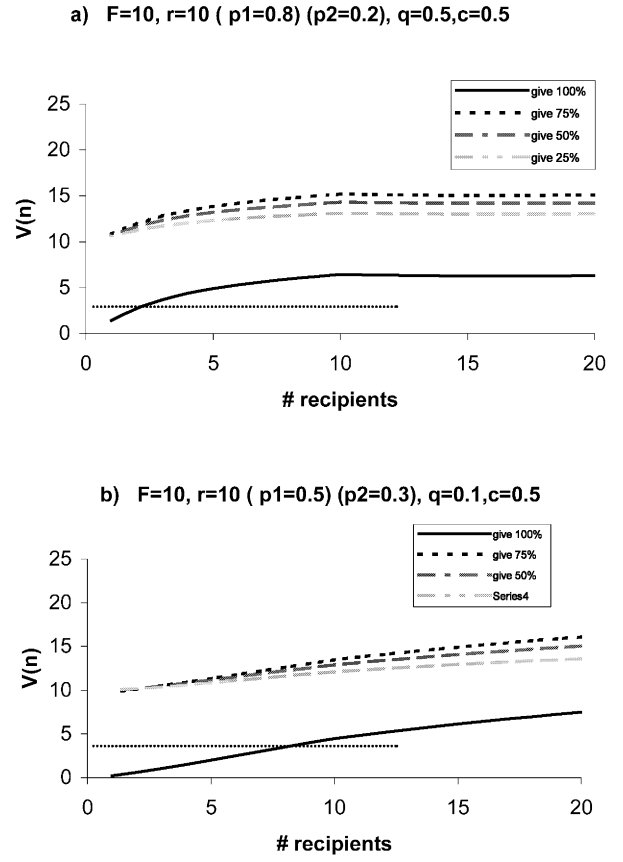

a)   F=10, r=10 (p1=0.8) (p2=0.2), q=0.5,c=0.5

b)   F=10, r=10 (p1=0.5) (p2=0.3), q=0.1,c=0.5

Fig. 4a–b Simulations of the sharing breadth-depth model. Similar to Fig. 3b, c, except resource package size is reduced, F=10, and p_1=0.5, and p_2=0.3 in (**b**). *Horizontal line* represents the expected value if none is given away

calculate the minimal probability that makes sharing a better option than hoarding:

$$(F - A)^c + n \left(\frac{PA}{n} \right)^c > F^c \tag{6}$$

$$\Rightarrow p_{\min} > \frac{n}{A} \left(\frac{F^c - (F - A)^c}{n} \right)^{1/c} \tag{7}$$

Appendix 2

For all simulations, F=100, N=20, and r=10. Figures 3a–c allow for half the individuals to reciprocate with p_1=0.8, while the other half reciprocate with p_2=0.2. In Fig. 4, p_1=0.5 and p_2=0.3. In each graph, I consider the acquirer giving 25%, 50%, 75%, and 100% of their acquisition to anywhere from 1 to 20 recipients. Several diminishing value functions, including the natural logarithmic function and power functions of degree between 0.3 and 0.6 were evaluated. The value function used for presentation is a square root function (c=0.5), although other value functions give similar qualitative results. In terms of identifying an intermediate optimal breadth and depth, the
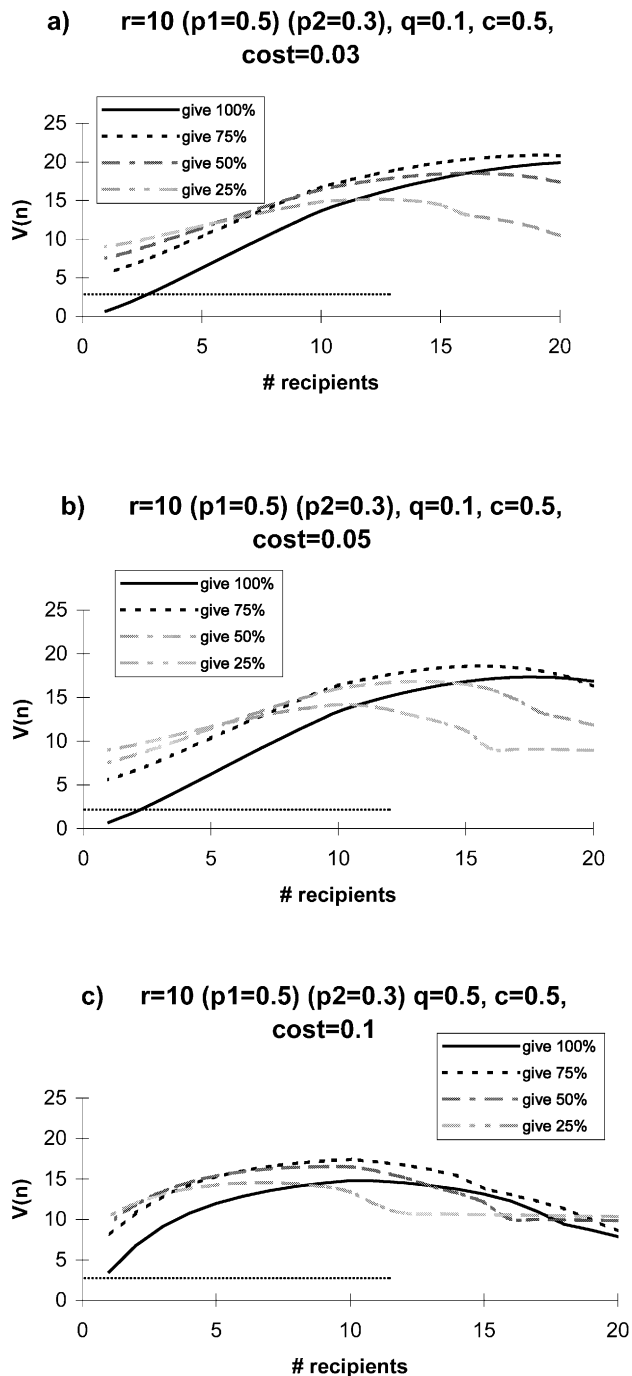
a)   r=10 (p1=0.5) (p2=0.3), q=0.1, c=0.5, cost=0.03

b)   r=10 (p1=0.5) (p2=0.3), q=0.1, c=0.5, cost=0.05

c)   r=10 (p1=0.5) (p2=0.3) q=0.5, c=0.5, cost=0.1

Fig. 5a–c Graphs of $V(n)$ with linear cost function ($n \times$ cost). Similar to Fig. 4b, with a cost **a** $c=0.03$, **b** $c=0.05$. In part **c** the cost $c=0.1$ and probability of simultaneous returns $q=0.5$

square root function will be more conservative than the logarithmic function because the former is less steeply declining than the latter. The dashed horizontal line in each figure gives the baseline benefit $(F-A)^c$ from hoarding. Return values $V(n)$ are calculated according to Eqs. 4 and 5. See also Fig. 5. Details about the figures are given in the text.

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