The evolution of contingent cooperation

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1. Introduction

The critical aspect of reciprocal altruism (RA) is that cooperation by ego is conditional upon the cooperation of others. The most popular form of RA is the tit-for-tat (TFT) strategy, where an act of cooperation by ego with individual Y at time t is based on Y’s cooperation with ego at time t-1 (Axelrod and Hamilton 1981). Although the strategy may be based on recollections of past behavior, its stability and robustness against other strategies depends on future expectations (ibid). This conditionality or “contingency” that defines RA requires discrimination based on a system of score-keeping (Hill and Kaplan 1993). The details underlying this conditionality have been the subject of controversy among those attempting to
test predictions of theoretical models in field populations. Despite the importance of contingency for testing whether pro-social interactions are best regarded as RA, and for understanding the proximate means by which RA may operate in different species under a variety of contexts, only a small proportion of the RA literature focuses on defining and testing contingency, the majority of which focuses on non-human primates (e.g. Brosnan and de Waal 2002, de Waal and Luttrell 1988, Rothstein and Pierotti 1988).

Among humans and non-human primates, the study of intra-group food transfers has produced a rich literature on the biology of altruism (for review and references see Brosnan and de Waal 2002, Gurven 2004b, Rose 1997, Winterhalder 1997). Explorations of RA among humans in modern populations, in terms of both behavior and psychology, often rely on a long, selective history of RA in the context of a hunting and gathering lifestyle (e.g. Cosmides and Tooby 1992, Hoffman, McCabe, and Smith 1998, Ridley 1996). RA is viewed as crucial for survival, given the potential for high fluctuations in daily food acquisition, and the obvious fitness benefits to resource pooling (Winterhalder 1986). However, among researchers working among hunter-gatherers and small-scale forager-farmers, there is little consensus about the importance of RA in structuring decisions about food production and distribution. As an alternative to RA, instances of widespread food sharing have been explained as a result of costly signaling (Bird 1999, Hawkes, O'Connell, and Blurton Jones 2001, Smith and Bliege Bird 2000), and as passive transfers via tolerated scrounging (Blurton Jones 1987, Hawkes 1993). These models differ in their assumptions about underlying motivations, mechanisms, and payoff structure. Whether RA or these other models best explain sharing practices affects our understanding of the sexual division of labor, origins of the nuclear family, and the evolution of the human life course (Bird 1999, Gurven 2004b, Hawkes et al. 1998, Kaplan et al. 2000). The
existence of RA supports the argument that men’s hunting is primarily a subsistence strategy consistent with the goal of family provisioning, rather than solely a means to achieve extra-marital reproductive success (see Winterhalder 2000; Bird and Hawkes 2003; Gurven 2004). Despite the importance of sharing for resolving these and other questions pertaining to cooperation, few empirical tests of RA have been done. Any test of RA requires an analysis of contingency. Explicit tests of contingency in transfers have been published only among the Yanomamo (Hames 2000), Hiwi (Gurven et al. 2000a), Ache (Gurven, Hill, and Kaplan 2002), and Meriam (Bliege Bird et al. 2002). Even with these few tests, a systematic treatment of contingency and RA has yet to be developed.

Several problems have plagued the measurement and interpretation of contingency as used in field studies. First, conditional acts of cooperation may be artifacts of symmetrical relationships, such as biological kinship or spatial proximity, among social actors, rather than calculated reciprocity. Thus, some sharing may occur only because some recipients are neighbors or close kin. We should be careful to distinguish such giving from calculated reciprocity (ibid). Classic cases of RA, such as blood sharing in vampire bats (Wilkinson 1984) and allogrooming in impala (Hart and Hart 1992), have since been labeled as instances of symmetry-based, as opposed to calculated, reciprocity (Brosnan and de Waal 2002). Second, acts of defection, and subsequent retaliation, require actors to identify and distinguish acts of cooperation from non-cooperation. However, acts of non-cooperation may sometimes be unintended, due to mistakes, noise, or phenotypic constraints. When errors occur or limitations exist, or when cooperation occurs in degrees rather than as all-or-nothing acts, greater levels of imbalance may be tolerated (Frean 1996, Wu and Axelrod 1995). Third, many measures of contingency are only statistical correlations and do not necessarily indicate a causal connection.
between acts done in one time period, and those after some subsequent delay. Fourth, not all studies distinguish between behaviors which are contingent within the context of dyadic interactions and those at the larger level of the population. For example, Hawkes, O’Connell and Blurton Jones (2001) test contingency by examining quantities of food $Y$ receives from all others based on how much $Y$ gave away to all others. This has been labeled “general” as opposed to “specific” contingency (Gurven et al. 2001). The focus on general contingency is problematic because only specific contingency can distinguish reciprocal altruism from other forms of giving (Hill and Kaplan 1993).

This paper first defines and operationalizes several forms of contingency which may exist in traditional non-market food sharing systems. It attempts to add psychological and ecological realism to standard mathematical treatments of cooperation and altruism. I then test for the existence of contingency among two groups of forager-agriculturalists, the Ache of Paraguay, and the Hiwi of Venezuela, explore causal influences affecting imbalances in transfers among families, and discuss implications for our understanding of fairness in small-scale societies. By introducing a variety of standardized measures of contingency, and linking these to explicit theoretical issues, this paper hopes to spur future theory development and empirical tests.

1.1. Conceptualizing contingency in hunter-gatherers

1.1.1. Equal exchange, or strict TFT, is not the only form of RA

An increasing number of theoretical studies have shown that strict TFT may be rare, and is only one of many potentially stable strategies of contingent cooperation. When conditions vary among actors, or over time, unequal exchanges may be favored, even in the standard Prisoner’s Dilemma context (Boyd 1990, Winterhalder 1996). Recent applications of market theory and
bargaining have also shown that when supply and demand affect the utility or value of resources and services, the relative costs and benefits may differ across actors in ways that often lead to unequal outcomes (Boyd 1990, Gurven et al. 2000a, Nöe, van Schaik, and van Hooff 1991). Unequal exchange may be favored as long as the “bargain” struck by actors is better than the alternative of no bargain, and no exchange. Contingent cooperation therefore does not require exact balance.

Norms of contingency within a group provide culturally-specific definitions of defection, cheating, free-riding, and slacking (Gurven 2004b). These norms are often implicit, and may vary by resource, dyadic relationship or situation. Ethnographic accounts of conflicts and disputes governing food transfers consist largely of accusations of others’ failure to meet expectations of contingency, and others’ justification for failed expectations. Punishment, in the form of gossip, partner switching, share withholding, and ostracism, occurs usually only after a series of unequivocal defections (ibid).

1.2. Forms of contingency

Contingent cooperation is most likely when there are a large number of interactions among actors. To the extent that interactions only continue based on a perception of continued cooperation, the form of contingency described in a social contract should attempt to maximize benefits and minimize costs for most participants. The measures of exchange, and of contingency, used in sharing studies should not just be a matter of convenience, but should be chosen with consideration of underlying principles governing exchange relations in the first place. As described elsewhere, ultimate reasons for giving include short- and long-term risk-reduction, communication of intent, commitment, or underlying quality, and increased efficiency.
through economies of scale (Gurven 2004). Contingency is relevant when sharing occurs for the purpose of risk-reduction or to gain advantages from economies of scale. Display giving, or giving under pressure to only avoid a cost, does not entail any expectation of direct returns.

Sharing rules which govern redistribution without any direct concern for contingency are given in the first three rows of Table 1. These include random giving (#1.1), giving equally to everybody in the group (#1.2), or to those who first arrive at the site of distribution (#1.3). The first and third of these may be rare cross-culturally (Gurven 2004), while equal giving to everybody may occur under certain restrictive conditions of strong inter-dependence and small group size, or when giving for status display (see section 4).

[INSERT TABLE 1 HERE]

Norms of contingency are usually associated with cultural perceptions of “fairness” and “equity” in social relationships. The strictest, and perhaps easiest to measure, form of contingency is when individuals give food to specific others based on the absolute quantities of food given to them by those others (Table 1: row 2.1). This form of contingency is the least forgiving because any failure to reciprocate quantity for like quantity may be construed as some degree of defection. More forgiving forms of contingency may emphasize the longer-term value of social partners and of future cooperation, especially when there is uncertainty about others’ level of food production and of their intentions. For example, the “value” of others’ offerings may be more useful a currency than quantities (Table 1: row 2.4), where value represents the utility of a unit of food, which may diminish with each additional increment relative to household or local supply and demand (Winterhalder 1996).

A form of contingency where the unit of exchange is the percentage of production given to others, may be a closer measure of cooperative intent, assuming a certain level of production
(Table 1: row 2.2). This standardizes amounts exchanged based on differences in absolute production, regardless of underlying decisions, or reasons for differences in production across families. Another measure of intent may be the frequency of exchanges across pairs of families (Table 1: row 2.3). While these forms of contingency may not always result in ideal exchanges, they may be useful for gauging cooperative intent, which carries over during times of sickness or injury (Gurven et al. 2000b), and in other important domains.

A final form of contingency focuses on the inter-relationship between production and distribution. A receipt of food is a result of a donor’s production times the percentage given to the recipient. An individual hunter returns to camp empty-handed roughly 40% of the time if he is Ache, and 65% of the time if he is Hiwi. Even good hunters often return to camp empty-handed, and so may not always have an opportunity to share. Given that food production occurs away from residential camps, often by solitary individuals, pairs, or small groups, it is often difficult to directly observe whether others fail to produce food because of random “luck” or because of laziness, slacking, or a general failure to organize work time efficiently. It has been suggested that labor inputs may be just as, if not more important, than quantities produced when there are strong inter-dependencies among group members (Gurven et al. 2001, Hill 2002). Thus, labor-based contingency makes giving conditional upon labor and capital inputs (Table 1: row 3.1), which have the potential to positively impact other group members. The simplest example of this is for hunters (or distributors) to examine the number of hours or days spent hunting by other men. However, with divisions of labor by age, sex, and skill, comparison of hours spent only hunting may be a poor measure of total work effort. Some Ache men clear trails, others chop down trees for palm heart extraction, and women prepare campsites. For resource items whose production is subject to frequent random variation, quantity-based contingency may not
be the most reliable form of cheater-detection in all circumstances. For highly predictable resources, such as horticultural foods and gathered items, there is less uncertainty about production, and so quantity-based contingency may be a useful, simple gauge, especially in larger groups. With these foods, quantity also correlates strongly with time spent in production, or work effort.

All measures of contingency presented here assume pairwise social relations, even though the immediate context of distributions may be group-wide events. Although the strategic component of larger n-person production or distribution events involves more than a single pair of individuals or families, any particular food item is still exchanged among pairs of individuals. The complexity of sharing decisions is beyond the scope of this paper. It suffices to say that judgments of fairness by individual X regarding individual Y’s decision to give to X will be based on the social relationships between X and Y, the relationships between production and distribution, norms which assign social categories of individuals to receive shares, and the proximate context of distribution.

2. Materials and Methods

Details on methods and ethnographic descriptions of the Ache are given in Gurven et al. (2001) and Gurven, Hill, and Kaplan (2002), and of the Hiwi are given in Gurven et al. (2000a). I summarize these briefly here. Ache 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-hour observation blocks of all food distributions, consumption, and production of all members of 2 or 3 households. Each household was sampled in this manner for an average of 56 hours, 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 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.

Data on Hiwi foragers were collected at the Mahenemuthu settlement in Venezuela by A.M. Hurtado and K. Hill during the 1987-88 field season from December to February and in parts of the wet season from April to May. The Hiwi sample consists of 106 foragers organized into 37 nuclear families in 14 dwellings spaced about 100 meters along a levee of the Capanaparo River. On sample days, resource type, original package size, acquirer, weights of all pieces, and names of all recipients were recorded for every fifth resource brought back to camp amongst a group of families. This sample is biased towards those acquirers that lived relatively close to the anthropologists. Weights were measured in the same fashion as among the Ache. The data include a total of 141 sharing events.

All estimates of contingency are standardized parameter coefficients from linear regression analyses. The outcome variable is the summed transfers (amount, value, etc.) from family $A$ to family $B$, and the contingency estimate is the regression coefficient for the summed transfers from family $B$ to family $A$. A transfer from $B$ to $A$ occurs when any member of family $B$ transfers a food item to any member of family $A$. Summed transfers over the sample period will thus be greater than or equal to zero from any $A$ to any $B$. The regression estimate is used
rather than the Pearson correlation because only the magnitude of the coefficient defines an actual exchange rate between giving and receiving. Each analysis sums the total amount or value exchanged among pairs of families over the duration of the sample periods for each study. However, section 3.2 includes an analysis which examines the effect of giving by $A$ to $B$ during the first half of the sample period, on $A$’s receiving from $B$ during the second half of the sample period. Each family is paired with every other family, and because each pair of families yields two perfectly correlated data points, I randomly choose one pair of points in all analyses. Thus, data on 25 families yields $25 \times 24 = 600$ pairings, or 300 independent data points. Finally, all analyses control for kinship and physical proximity between households. Inter-household kinship is estimated as the closest coefficient of genetic relatedness among all members of two families. Proximity is measured as the distance in meters between any pair of households. Inclusion of these kinship and proximity insures that contingency is estimated independent of other symmetry-based causal influences which could lead to a spurious acceptance of contingent reciprocity.

3. Results

Table 2 lists four sets of contingency estimates for Ache and Hiwi, measured over the range of the entire sample period for each population, and controlling for kinship and proximity. Among Ache, contingency is given for transfers of forest foods brought back to Arroyo Bandera (e.g. meat, honey), cultigens (e.g. sweet manioc, corn, sweet potato), store-bought foods (e.g. bread, cooking oil), and all foods combined. Among Hiwi, contingency is given for meat, fish, other foods (e.g. fruits, roots), and all foods combined. Column 2 describes contingency as “quantity”, or the “# of kilograms of resource $x$ given by $A$ to $B$” associated with the same given
by $B$ to $A$ (see Table 1: 2.1). Column 3 describes contingency as “standardized”: “% of $A$’s production of $x$ given to $B$” and vice-versa (see Table 1: 2.2). Columns 4 and 5 describe contingency as “value”, where value is estimated as a natural log and square root function of quantities exchanged, respectively: “total value of resource $x$ given by $A$ to $B$” and vice-versa (see Table 1: 2.4). Finally, column 6 describes contingency as “frequency”, or the “# of times $A$ gave food to $B$” and vice-versa (see Table 1: 2.3).

[INSERT TABLE 2 HERE]

Table 2 shows strong evidence for contingency for meat and fish, but not for the resource category “other” among the Hiwi. For example, for every kg of meat and other foods given away to another family, 0.69 and 0.08 kgs are given back, respectively. Using the same resource types, for every percentage of meat and other production given away to a specific family, 37% and 13% is returned over the duration of the sample period. Most resource categories contain several forms of contingency which achieve statistical significance at typical levels. No single form of contingency is consistently the highest across groups or resource types. Among the Hiwi, quantity gives the highest estimate for meat and all resources combined, with log value yielding estimates close in magnitude. Fish exchanges are best described by standardized quantity. Among the Ache, frequency and log value show highest contingency estimates for forest foods and cultigens, with square root value the highest for all foods combined. Quantity is the highest measure for store-bought foods. Value-based contingency tends to be higher than quantity-based contingency among the Ache because families who gave greater quantities to other families received shares more frequently from those families. There is little difference between quantity- and value-based contingency among the Hiwi because those families who gave more food to other specific families also gave more frequently to them (Gurven 2004a). Hiwi economic
production tends to be more independent at the family level than among the Ache, and greater independence may account for less tolerance of imbalance among the Hiwi. However, the non-random sampling of Hiwi families and the crudeness of the value measures prevents any strong interpretations between groups.

The lack of contingency in non-meat items among the Hiwi is noteworthy. The roots and fruits that comprise over 40% of the Hiwi diet are the least transferred resources (Gurven et al. 2000a). A combination of high predictability, low variance in return rates, and synchronous acquisition across individuals makes reciprocal sharing of these resources unnecessary. Although carbohydrates are limiting macronutrients through much of the year, the marked seasonality of roots and other starches insures that variance in daily acquisition is very small across foragers. Thus, there are few variance-reduction benefits to reciprocal sharing of these foods. Alternatively, fruits are a small percentage of the diet among Ache at the reservation, while roots are non-existent. Cultigens among Ache are also predictable, but daily production may vary across individuals, and turn-taking associated with economies of scale due to fixed travel and processing costs can make reciprocal sharing of farm foods profitable (Gurven et al. 2001).

No consideration of “work effort”-based contingency was taken before the Hiwi or Ache studies were conducted. I can only test whether Hiwi and Ache who spent more days or hours foraging received more food from all other individuals. These measures are therefore akin to “general” contingency, rather than pairwise contingency measures of relative work effort in sharing decisions. Among Hiwi, families whose members spent more time foraging (days or total hours) received more food from other group members (correlation between total hours spent foraging and total food received from members of other families, $r=0.616, p<0.0001$). While
work effort and food production are highly correlated ($r=0.630$, $p<0.0001$), total hours spent foraging is a still a highly significant predictor of food shares received from others even after controlling for kilograms of food produced and family size (partial $r=0.435$, $p<0.05$). Similar results obtain if we confine food receipt to meat or fish. Among Ache, the only work effort measure available is foraging labor of men. Controlling for total family food production, families of men who spent more days in the forest hunting and foraging did not receive more food from others ($r=-0.219$, $p=0.27$). They also did not receive more foods from others returning to the settlement after foraging treks ($r=0.137$, $p=0.50$).

3.1. Predictors of imbalance

I examine the effects of several causal influences on the extent of imbalance in quantity exchange among the Ache. I define “imbalance” as the total kilograms $A$ gave $B$ minus the total kilograms $B$ gave $A$ over the sample period. Positive values of imbalance therefore favor $B$ at the expense of $A$. All else being equal, larger families and families who produce less food will show greater demand for food. Thus, I predict that family size will vary positively and negatively for donor and recipient families, respectively. Additionally, older individuals may display more political clout and thus be able to manipulate the sharing system to their advantage. A simple prediction from bargaining theory is that age of the oldest member of the recipient family should vary positively with imbalance. Table 3 reports the results of a multiple regression analysis that includes family food production, family size, and age of the oldest member of the recipient family, as well as closest biological kinship (measured by the coefficient of genetic relatedness) and spatial proximity (measured in meters) between houses of donor and recipient families. Standardized parameter estimates are given for ease of comparison across variables. The
strongest predictors of imbalance are the levels of production exhibited by donor and recipient families. Controlling for other variables in the model, high producing donors give more than they receive and low producing recipients receive more than they give. This model accounts for 20% of the variation in exchange imbalances. Similar effects are found for donor and recipient family production when examining imbalance in forest foods, cultigens, and store-bought foods (not shown). Neither kinship nor distance is significant in this model, due to the symmetrical nature of these variables with respect to positive and negative values of imbalance. When imbalance is measured without regards to the direction (as the absolute value of the difference between amounts exchanged across families), or when only positive imbalances are considered, kinship and distance significantly vary with imbalance (partial $\beta= 4.334$, std. est.=0.11, $p<0.05$ for kinship; partial $\beta= -0.015$, std. est.=-0.13, $p<0.05$ for distance). Thus, close kin and close neighbors show higher levels of imbalance than distant kin or unrelated families, and distant neighbors. Hames (1987b) reports a similar finding with respect to kinship and imbalances in garden labor exchange.

[INSERT TABLE 3 HERE]

3.2. *Time-delayed contingency*

All of the estimates of contingency in Table 2 are based on summed transfers, value, or frequency of exchanges over entire sample periods. Only the Ache study has a sufficient sample size, time duration, and randomized selection methodology to allow a crude time-dependent estimate of contingency which more accurately represents the concept. I arbitrarily split the sample into two time periods of 28 and 27 sample days--Feb. 9, 1998 thru March 12, 1998, and March 13-April 23. This division represents the date on which an average of 49% of the sharing data for each family had been collected, rather than the chronological midpoint of the sample
period. Contingency in Table 4 refers to the relationship between amounts, value, or frequencies of transfers by $A$ towards $B$ during time period 1 and those by $B$ towards $A$ during time period 2. As in Table 2, all estimates control for kinship and proximity.

[INSERT TABLE 4 HERE]

The magnitudes of contingency estimates are smaller than those given in Table 2, but are still statistically significant at typical levels. Frequency and value show highest magnitudes for all resources combined, cultigens, and for forest foods. It is relevant here to mention that the partial Pearson correlations are 10-100% greater in magnitude than the parameter estimates given in Tables 3 and 4. Elsewhere contingency has been reported as a Pearson correlation, rather than as parameter estimates from regression analysis. While these two measures are usually similar in magnitude, they are more likely to diverge in multivariate analyses.

4. Discussion and Conclusion

This paper has provided evidence of significant contingency in food exchange for both Ache and Hiwi, even though the form and magnitude of contingency may be variable across populations, resource types, and families. This is the first study to examine multiple measures of contingency, and to incorporate value, and not just quantities, of resources into tests of reciprocal altruism. To date, theoretical discussions of sharing often involve exchanges of value, even though all past empirical tests have focused on exchanges of quantity. The estimates of value presented are admittedly crude, but call attention to the diminishing utility of large quantities of food shares (Gurven 2004a, Winterhalder 1996). Measures of value may better capture the implicit bargains people make in negotiating time-dependent exchanges of food, especially when strong economic interdependencies exist among individuals. An emphasis on value suggests that
future studies must pay attention to time-varying differences in supply and demand of specific resources. This additional information at the time sharing occurs may provide insight into how immediate context affects sharing, and how decisions are made. Study of supply and demand, and other factors affecting the bargaining power of individuals may also provide insight into the conditions where exchange imbalances are generated, maintained, and tolerated. In this study, value appears to level imbalances more among the Ache than among the Hiwi, perhaps due in part to the greater interdependencies in food production among the Ache.

Beyond quantity or value, I suggest that a labor-based contingency that relies on labor and capital inputs into joint or inter-dependent production may represent a type of bargain that is consistent with psychological and cultural evidence. A series of experiments in psychology and economics have found empirical support for the notion that labor inputs affect distributional decisions (Güth 1994, Königstein 2000, Selten 1978). Unlike many economics experiments which only examine the distribution of windfall endowments, these experiments require players to work and produce the endowments which are subsequently divided. The emphasis on windfalls misses the crucial contextual link between production and distribution, and so windfall experiments are likely to provide insight into only one narrow domain of giving. Nonetheless, an increasing number of experiments have also shown that concerns over fairness affect people’s emotions, attitudes, and behavior towards distribution rules and perceptions of equity (see Fehr and Gächter 2002, Fehr and Schmidt 1999). Thus, contingency is not just a statistical phenomenon, but instead reflects an underlying psychology, and manifests itself in the form of cultural norms. Ethnographic descriptions of foraging cultures often de-emphasize score keeping in social relationships, and instead focus on generalized exchange that pays off only in the long-term. Alternative forms of contingency, such as those discussed in this paper, may begin to
bridge the gap between the short-term calculus of reciprocal altruism and the kinds of long-term social relationships emphasized in cultural norms.

I have shown that Hiwi who spend more time foraging are rewarded with more food from others. This relationship was not found with the Ache. However, the measure of labor I used for the Ache only considered foraging effort of men, while game represents less than 10% of the calories consumed at the Arroyo Bandera settlement. Sharing on foraging treks is more widespread than at the settlement. Although sharing has been described as unconditional on foraging treks, it is likely that quantity or value-based contingency measures do not capture the social contract associated with high-risk game in the forest. The sharing pattern of the Ache while foraging is a good candidate for labor-based contingency. Indeed, Hill (2002) has shown that men and women spend up to 17% of their foraging time doing activities that only increase the caloric return rate of other individuals. There are no cases of individuals refusing to work, and teenagers are sometimes told that they must work in order to receive food (Gurven et al. 2002; Hill 2002).

Although the majority of the diet consumed during foraging treks is high-risk game resources, gathered foods and farm foods at Arroyo Bandera are highly predictable. The sharing of these predictable foods therefore does not reduce risk, but more likely represents an economy of scale. Due to the fixed costs of travel and transport, individuals take turns acquiring or harvesting more food than they or their family members can consume (Hames 1987a). In order for such a system to be efficient, contributing members must take turns and reliably produce food. Thus, while sharing of these foods may also be based on the labor inputs of others, the quantities of foods produced is strongly correlated with time spent engaged in productive labor, and so quantity is probably the best indicator of trust or commitment to the sharing system.
There do not appear to be economies of scale in fruit or root collection among Hiwi, even though women occasionally exchange equal quantities of roots when there are no immediate advantages to doing so (Gurven et al. 2000a).

Any particular social contract will not benefit everyone equally. For example, high producers may only benefit when sick or injured (Gurven et al. 2000b, Sugiyama and Chacon 2000). The result that high producers are more likely to give than receive, when compared with low producers, is consistent with the notion that short-term costs of imbalance act as premiums for a form of social insurance. The premiums may pay off only during difficult times and so on average, imbalances in quantities exchanged are likely. As shown in section 3.2, imbalances are more prevalent among close kin and neighbors. Kin and neighbors are most likely to be committed to engage and invest in long-term relationships. It remains to be seen whether the estimated levels of contingency are alone sufficient to motivate high levels of production, or whether other incentives are necessary. High producers may gain if high production acts as an honest signal of phenotypic quality, which leads to greater mating opportunities (Smith and Bliege Bird 2000), or of cooperative intent or commitment which may lead to better social partners (Frank 1988, Gurven et al. 2000b, Smith and Bleige Bird in press). Additionally, high producers may be able to directly trade surplus resources for other goods or services. Thus, other mechanisms may encourage higher levels of production than warranted by just contingency itself.

Further theoretical and empirical study of contingency will be necessary for a detailed understanding of how reciprocal altruism operates in populations, especially when other motivations, incentives and obligations offer competing demands on individuals’ production. Although ecological arguments have been made about the role of intra- and inter-forager
variance in favor of more or less sharing (e.g. Winterhalder 1986), underlying determinants of such variation, apart from stochastic factors, have not been explored. Differential use of time, skill and knowledge, and intent are some examples of additional determinants of variation in production. Variance due to uncontrollable factors may favor more tolerance of imbalances, and more value- or labor-based contingency. Variance due to decisions under more direct personal control should be more associated with quantity-based contingency because motivated individuals focusing on predictable resources can be more self-reliant and because failure by others to produce sufficient quantities of food is less excusable or worthy of assistance.

Little is known about how sharing norms or rules of thumb (Table 1) develop, and are maintained or change over time. Much ethnographic evidence suggests that expected patterns of distribution are importantly linked to production in a structured way. Resource flows are linked to both the production of food and more generally to the production of offspring, via the coordinated actions of individuals within and across families involved in sharing networks. With increased self-sufficiency at the household and extended household level, as in many forager-horticultural populations, contingency may depend more on quantity or value. A dependence on quantity or value may even be favored among foragers relying on unpredictable resources if group size is fairly large, such that the monitoring of labor inputs may be difficult. Even in larger groups, people may share loosely with close kin and friends who live in close proximity, and more conditionally with acquaintances living further away. However, in many small foraging groups with interdependencies, “fair” distribution norms should be based on the labor contributions of their members.
TABLE 1. Unconditional and conditional sharing rules governing resource distribution decisions. Formulae reflect the operationalization of specific contingency variables as described in text. Total quantities given from $A$ to $B$ are shown using double summations. The inner summation describes the amounts given by a particular $A$ to each specific recipient, $B$, during a single distribution. The outer summation applies the inner summation to all distributions where a particular $A$ was acquirer. The last column is the same but describes transfers from $B$ to $A$.

<table>
<thead>
<tr>
<th>#</th>
<th>Sharing rule</th>
<th>Contingency?</th>
<th>Type</th>
<th>$A$ to $B$</th>
<th>$B$ to $A$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1)</td>
<td>give to all others randomly</td>
<td>No</td>
<td></td>
<td>$\sum_{i_1} \sum_{j_B} amt_{i_B} = \sum_{i_2} amt_{i_A}$</td>
<td></td>
</tr>
<tr>
<td>1.2)</td>
<td>give to all others equally</td>
<td>No</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1.3)</td>
<td>give to all others first-come first-serve</td>
<td>No</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2.1)</td>
<td>give to those who give more quantity to you</td>
<td>Yes</td>
<td>Amounts</td>
<td>$\sum_{i_1} \sum_{j_B} amt_{i_B} = \sum_{i_2} amt_{i_A}$</td>
<td>$\sum_{i_2} amt_{i_A}$</td>
</tr>
<tr>
<td>2.2)</td>
<td>Give to those who give you a larger percentage of their production</td>
<td>Yes</td>
<td>Standard</td>
<td>$\sum_{i_1} \sum_{j_B} amt_{ij} = \sum_{i_2} amt_{ij}$</td>
<td>$\sum_{i_2} amt_{ij}$</td>
</tr>
<tr>
<td>2.3)</td>
<td>Give to those who give more frequently to you</td>
<td>Yes</td>
<td>Frequency</td>
<td>$\sum_{i_1} \sum_{j_B} \ln(amt_{i_B}) = \sum_{i_2} \ln(amt_{i_A})$</td>
<td></td>
</tr>
<tr>
<td>2.4)</td>
<td>Give to those who give more &quot;value&quot; to you</td>
<td>Yes</td>
<td>Value1</td>
<td>$\sum_{i_1} \sum_{j_B} \sqrt[3]{amt_{i_B}} = \sum_{i_2} \sqrt[3]{amt_{i_A}}$</td>
<td>$\sum_{i_2} \sqrt[3]{amt_{i_A}}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Value2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3.1)</td>
<td>Give to those who contribute inter-dependent labor</td>
<td>Yes</td>
<td>Labor</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2. Four types of contingency estimates for (a) Hiwi and (b) Ache. Quantity measures kilogram exchanges across pairs of families. Standardized quantity examines the percentages of food production exchanged across family pairs. Value1 and value2 examine total value exchanged across families, where value is measured as the \( \ln(\text{quantity}) \) and \( \sqrt{\text{quantity}} \). Frequency examines the number of times food was given across family pairs. Ache sample of 24 families yields 512 data points, or \( n=276 \) independent data points. The Hiwi sample only includes families which were adequately sampled, due to non-random sampling in the Hiwi study, and so sample sizes vary (\( n=55, 71, 181, 419 \) for meat, fish, other, and all foods, respectively; see Gurven et al. (2000a) for details.

<table>
<thead>
<tr>
<th>Resource type</th>
<th>Quantity (kg-kg)</th>
<th>Standard Quantity (%-%)</th>
<th>Value1 (ln)</th>
<th>Value2 (sqrt)</th>
<th>Frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>a) Hiwi</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meat</td>
<td>0.690</td>
<td><strong>0.369</strong></td>
<td>0.482</td>
<td>0.239</td>
<td>0.267</td>
</tr>
<tr>
<td>Fish</td>
<td>0.162</td>
<td><strong>0.498</strong></td>
<td>0.329</td>
<td>0.206</td>
<td>0.248</td>
</tr>
<tr>
<td>Other</td>
<td>0.078</td>
<td>0.132</td>
<td>0.072</td>
<td>0.049</td>
<td>-0.026</td>
</tr>
<tr>
<td>ALL</td>
<td>0.293</td>
<td><strong>0.205</strong></td>
<td>0.203</td>
<td>0.154</td>
<td>0.159</td>
</tr>
<tr>
<td><strong>b) Ache</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>0.043</td>
<td>0.020</td>
<td><strong>0.226</strong></td>
<td>0.184</td>
<td>0.234</td>
</tr>
<tr>
<td>Cultigens</td>
<td>0.206</td>
<td><strong>0.261</strong></td>
<td><strong>0.334</strong></td>
<td><strong>0.314</strong></td>
<td>0.370</td>
</tr>
<tr>
<td>Storebought</td>
<td>0.476</td>
<td><strong>0.332</strong></td>
<td><strong>0.339</strong></td>
<td><strong>0.336</strong></td>
<td>0.132</td>
</tr>
<tr>
<td>ALL</td>
<td>0.207</td>
<td><strong>0.253</strong></td>
<td><strong>0.531</strong></td>
<td><strong>0.647</strong></td>
<td>0.511</td>
</tr>
</tbody>
</table>

***p<0.0001, **p<0.001, *p<0.05
TABLE 3. Predictors of imbalance (total kilograms of food $A$ gave to $B$ minus total kilograms of food $B$ gave to $A$) for the Ache sample.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>predicted direction</th>
<th>partial estimate</th>
<th>partial standard estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family size of $B$</td>
<td>$+$</td>
<td>0.483</td>
<td>0.14</td>
</tr>
<tr>
<td>Family size of $A$</td>
<td>$-$</td>
<td>-0.633</td>
<td>-0.17</td>
</tr>
<tr>
<td>Age of oldest member of $B$</td>
<td>$+$</td>
<td>0.028</td>
<td>0.06</td>
</tr>
<tr>
<td>$B$'s total production</td>
<td>$-$</td>
<td>-0.045</td>
<td>-0.41</td>
</tr>
<tr>
<td>$A$'s total production</td>
<td>$+$</td>
<td>0.044</td>
<td>0.37</td>
</tr>
<tr>
<td>Biological kinship, $r$</td>
<td>$+$</td>
<td>-1.527</td>
<td>-0.03</td>
</tr>
<tr>
<td>Physical proximity (meters)</td>
<td>$-$</td>
<td>0.007</td>
<td>0.05</td>
</tr>
</tbody>
</table>

Note: Model $F=9.43$, $p<0.0001$, df=7, n=276, $R^2=0.20$

***$p<0.0001$, **$p<0.001$, *$p<0.05$
TABLE 4. Contingency estimates for Ache where giving by $A$ to $B$ in time period 1 is regressed on giving by $B$ to $A$ in time period 2 (see text for details). Sample size $n=276$ for each of the analyses.

<table>
<thead>
<tr>
<th>Resource type</th>
<th>kg-kg</th>
<th>%-%</th>
<th>ln(kg)-</th>
<th>sqrt</th>
<th>frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>0.008</td>
<td>0.051</td>
<td>0.023</td>
<td>0.030</td>
<td>0.050</td>
</tr>
<tr>
<td>Cultigens</td>
<td>0.057</td>
<td>0.145</td>
<td>0.112</td>
<td>0.136</td>
<td>0.224</td>
</tr>
<tr>
<td>Storebought</td>
<td>0.001</td>
<td>0.157</td>
<td>0.029</td>
<td>0.043</td>
<td>0.053</td>
</tr>
<tr>
<td>ALL</td>
<td>0.095</td>
<td>0.081</td>
<td>0.160</td>
<td>0.188</td>
<td>0.261</td>
</tr>
</tbody>
</table>

***p<0.0001, **p<0.001, *p<0.05
References Cited


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1 I would like to thank the Ache of Arroyo Bandera and the Hiwi of Mahenemuthu for their kindness and support. I also thank Ray Hames, Eric Smith, Bruce Winterhalder, and two anonymous reviewers for their useful comments and suggestions.

2 A symmetrical relationship occurs when the relationship between $A$ and $B$ is identical to that between $B$ and $A$. 