

The Evolution of Contingent Cooperation

Michael Gurven

Department of Anthropology, University of California,
Santa Barbara, CA 93106, U.S.A. (gurven@anth.ucsb.edu).
21 IX 05

With CA+ supplements

Reciprocal altruism has been proposed as a foundation of cooperation in humans. The core feature of reciprocity is the contingent relationship between acts of giving and receiving among social partners. However, contingency has remained largely an elusive concept with little empirical scrutiny. Food sharing in small-scale, nonmarket societies is a classic context for examining conditional cooperation. The debate concerning whether food sharing is a crucial component of household provisioning or a form of display geared toward personal benefit hinges on whether food is given conditionally. Several forms of contingency are defined here, and it is shown that a significant contingency relationship exists in food exchange among two groups of forager-agriculturalists, the Ache of Paraguay and the Hiwi of Venezuela. Exchange imbalances tend to favor lower-producing families, close kin, and nearby neighbors. These results have implications for understanding fairness in forager societies.

The critical aspect of reciprocal altruism is that cooperation by ego is conditional upon the cooperation of others. The most popular form of reciprocal altruism is the tit-for-tat strategy, in which 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 depend on expectations for the future. The conditionality or "contingency" that defines reciprocal altruism 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 prosocial interactions are best regarded as reciprocal altruism and for understanding the proximate means by which reciprocal altruism may operate in different species in a variety of contexts, only a small proportion of the literature, most of this focusing on non-human primates, is devoted to defining and testing contingency.

Among humans and nonhuman primates, the study of intragroup food transfers has produced a rich literature on the biology of altruism (for review and references see Brosnan

and de Waal 2002; Gurven 2004*b*; Rose 1997; Winterhalder 1997). Explorations of reciprocal altruism, in terms of both behavior and psychology, among humans in modern populations often rely on a long selective history of the practice in the context of the hunting and gathering lifestyle (Cosmides and Tooby 1992; Hoffman, McCabe, and Smith 1998). Reciprocal altruism is viewed as crucial for survival, given the potential for high fluctuations in daily food acquisition and the obvious fitness benefits of resource pooling (Winterhalder 1986). There is little consensus, however, about its importance in structuring decisions about food production and distribution. Alternatively, 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 structures. Determining which of these models best explains sharing is important for our understanding of the sexual division of labor, the origins of the nuclear family, and the evolution of the human life course (Bird 1999; Gurven 2004*b*). The existence of reciprocal altruism 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 extramarital reproductive success. Despite the importance of sharing for resolving these and other questions, few empirical tests of reciprocal altruism have been conducted. Any such test requires an analysis of contingency, and explicit tests of contingency in transfers have been published only for the Yanomamo (Hames 2000), the Hiwi (Gurven et al. 2000*b*), the Ache (Gurven, Hill, and Kaplan 2002), and the Meriam (Bliege Bird et al. 2002). No systematic treatment of contingency and reciprocal altruism has yet been developed.

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

Theoretical studies have increasingly shown that strict tit-for-tat 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 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. 2000*b*; 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. These norms are often implicit and may vary by resource, dyadic relationship, or situation (Gurven 2004*b*). Ethnographic accounts of conflicts and disputes governing food transfers consist largely of charges of others’ failure to meet expectations of contingency and others’ justifications for that failure. Punishment in the form of gossip, partner switching, share withholding, and ostracism usually occurs only after a series of unequivocal defections.

Contingent cooperation is most likely when the number of interactions among actors is large. To the extent that interactions continue only when there is 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 be chosen with consideration of the principles governing exchange relations. 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. 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 only to avoid a cost does not entail any expectation of direct returns. Sharing rules which govern redistribution without any direct concern for contingency include random giving, giving equally to everyone in the group, and first-come first-served (table 1). The first and third of these may be rare cross-culturally (Gurven 2004*b*), while equal giving to everyone may occur under certain restrictive conditions of strong interdependence and small group size or for the purpose of status display.

Norms of contingency are usually associated with cultural perceptions of “fairness” and “equity” in social relationships. The strictest form of contingency and perhaps the easiest to measure is the giving of food to specific others on the basis of the absolute quantities of food received from those others. This form of contingency is the least forgiving; any failure to reciprocate quantity for like quantity may be construed as some degree of defection. A form of contingency in which 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. This standardizes amounts exchanged on the basis of differences in absolute production, regardless of underlying decisions or reasons for differences in production across families. Another measure of

Table 1. Rules Governing Resource Distribution Decisions

Sharing Rule	Contingency?	Type
Give to all others randomly	No	
Give to all others equally	No	
Give to all others on a first-come first-served basis	No	
Give to those who give you more (quantity)	Yes	Quantity
Give to those who give you a larger percentage of their production	Yes	Standardized quantity
Give to those who give you more “value”	Yes	Value1
Give to those who give more frequently to you	Yes	Value2
Give to those who contribute interdependent labor	Yes	Frequency
	Yes	Labor time

cooperative intent may be the frequency of exchanges across pairs of families. Other 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, 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, may be a more useful currency than quantity (Winterhalder 1996).

A further form of contingency focuses on the interrelationship between production and distribution. Here receipt of food is the product of the giver’s production and the percentage of it that is given to others. A hunter returns to camp empty-handed roughly 40% of the time if he is Ache and 65% of the time if he is Hiwi. Given that food production occurs away from residential camps and often involves solitary individuals, pairs, or small groups, it is often difficult to 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 at least as important as quantities produced when there is strong interdependence among group members (Gurven et al. 2001; Hill 2002). Thus, labor-based contingency makes giving conditional upon labor and capital inputs, which have the potential to 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 the measures of contingency presented here assume pairwise relations even though the immediate context of a distribution may be a groupwide event. Although the strategic component of n -person events involves more than a single pair of individuals, any particular food item is still exchanged by a pair. The complexity of sharing decisions is beyond the scope of this paper. Suffice it to say that judgments of fairness by X regarding Y 's decision to give to X will be based on the social relationship between X and Y , the relationship between production and distribution, norms which designate categories of individuals as receivers of shares, and the proximate context of distribution.

Materials and Methods

Details on methods and ethnographic descriptions are given in Gurven et al. (2001) and Gurven, Hill, and Kaplan (2002) for the Ache and in Gurven et al. (2000*b*) for the Hiwi. Ache data were collected by W. Allen-Arave and me in the reservation of Arroyo Bandera ($n = 380$ food distributions, 121 individuals, 23 nuclear-family-based households) over 55 sample days between February and May 1998. Data on Hiwi foragers were collected by A. M. Hurtado and K. Hill in the Mahenemuthu settlement in Venezuela (141 sharing events, 106 foragers, 37 nuclear families in 14 dwellings spaced about 100 m apart along a levee of the Capanaparo River) over five months during 1987–88.

All estimates of contingency are standardized parameter coefficients from linear regression analyses. The outcome variable is the summed transfers (quantity, 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 B transfers a food item to any member of A. Each analysis sums the quantities or values exchanged among pairs of families over the duration of the sample periods for each study (but see below). Because each pair of families yields two perfectly correlated data points, I randomly chose one pair of points in all analyses. Thus, data on 25 families yield $25 * 24 = 600$ pairings, or 300 data points.

All analyses control for kinship and physical proximity between households. Interhousehold kinship is estimated as the

closest coefficient of genetic relatedness among all members of two families. Physical proximity is measured as the distance in meters between any pair of households. The inclusion of kinship and proximity ensures that contingency is estimated independently of other symmetry-based causal influences which could lead to a spurious acceptance of contingent reciprocity.

Results

Four sets of contingency estimates have been calculated for each group (table 2). For Ache, contingency is estimated 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. For Hiwi, contingency is estimated for meat, fish, other foods (e.g., fruits, roots), and all foods combined. There is strong evidence for contingency for meat and fish but not for the resource category “other” among the Hiwi. For example, for every kilogram of meat and other foods given to another family, 0.69 and 0.08 kilograms, respectively, are given back. Using the same resource types, for every percentage of meat and other production given to another family, 37% and 13%, respectively, are returned. Most resource categories show several forms of contingency achieving 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 that are similar in magnitude. Fish exchanges are best described by standardized quantity. Among the Ache, frequency and log value show the highest contingency estimates for forest foods and cultigens, with square-root value being the highest for all foods combined. Quantity gives the highest estimate for store-bought foods. Value-based estimates of contingency tend to be higher than quantity-based ones 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 specific others also gave to them more frequently (Gurven 2004*a*). 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. However, the nonrandom sampling of Hiwi families and the crudeness of the value measures preclude any strong between-group interpretation.

The lack of contingency in nonmeat items among the Hiwi is noteworthy. The roots and fruits that make up over 40% of the Hiwi diet are the least transferred resources (Gurven et al. 2000*b*). 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

Table 2. Contingency Estimates

Resource Type	Partial Regression Estimates				
	Quantity (kg-kg)	Standardized Quantity (%-%)	Value1 (ln)	Value2 (sqrt)	Frequency
Hiwi					
Meat	0.690**	0.369*	0.482*	0.239*	0.267*
Fish	0.162	0.498**	0.329*	0.206*	0.248*
Other	0.078	0.132	0.072	0.049	-0.026
All	0.293***	0.205**	0.203**	0.154**	0.159**
Ache					
Forest	0.043	0.020	0.226**	0.184**	0.234***
Cultigens	0.206**	0.261***	0.334***	0.314***	0.370***
Store-bought	0.476***	0.332***	0.339***	0.336***	0.132**
All	0.207***	0.253***	0.531***	0.647***	0.511***

*** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$

Note: All estimates control for kinship and spatial proximity between households. *Quantity* measure 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 (*quantity*) and $\sqrt{\text{quantity}}$. *Frequency* examines the number of times food was given across family pairs. The Ache sample of 24 families yields 512 data points or $n = 276$ independent data points. The Hiwi sample includes only families which were adequately sampled, and so sample sizes vary ($n = 55, 71, 181, 419$ for meat, fish, other, and all foods, respectively [see Gurven et al. 2000b for details]).

and other starches ensures 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 and roots nonexistent. 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).

Because no consideration of labor-time-based contingency was made before the 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 hours foraging received more food from other group members ($r = 0.616, p < 0.0001$). 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 food from others returning to the settlement after foraging treks ($r = 0.137, p = 0.50$).

When "imbalance" is defined 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 low-producing families should show greater demand for food. Thus, family size should vary positively and negatively for donor and recipient families, respectively. Additionally, older individuals may be able to manipulate the sharing system to their advantage. A simple prediction 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 and spatial proximity 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 because of the symmetrical nature of these variables with respect to positive and negative values of imbalance. When imbalance is measured without regard to the direction (as the absolute value of the difference between quantities 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 neighbors show higher levels of imbalance than distant kin or unrelated families and distant neighbors. Hames

Table 3. Predictors of Imbalance

Predictor Variable	Predicted Direction	Partial Estimate	Partial Standard Estimate
Family size of B	+	0.483	0.14*
Family size of A	–	–0.633	–0.17*
Age of oldest member of B	+	0.028	0.06
B's total production	–	–0.045	–0.41***
A's total production	+	0.044	0.37***
Biological kinship, r	+	–1.527	–0.03
Physical proximity (m)	–	0.007	0.05

*** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$

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

(1987b) reports a similar finding with respect to kinship and imbalances in garden labor exchange.

The contingency estimates 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, 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—February 9–March 12 and March 13–April 23, 1998. This division represents the date on which an average 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, values, or frequencies of transfers by A toward B during time period 1 and those by B toward A during time period 2. As in table 2, all estimates control for kinship and proximity.

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

Discussion and Conclusion

This paper has provided evidence of significant contingency in food exchange for both Ache and Hiwi, although its form and magnitude may vary across populations, resource types, and families. This is the first study to examine multiple measures of contingency and to incorporate values and not just quantities of resources into tests of reciprocal altruism. Whereas all past empirical tests have focused on exchanges of quantity, theoretical discussions of sharing often involve exchanges of value. The estimates of value presented here 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 im-

plicit bargains people make in negotiating time-dependent exchanges of food, especially when there is strong economic interdependence 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 may provide insight into how the 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 in which exchange imbalances are generated, maintained, and tolerated. In this study, value appears to level imbalances more among the Ache than among the Hiwi, perhaps in part because of the greater interdependence in food production among the Ache.

Beyond quantity or value, a contingency that relies on labor and capital inputs in joint or interdependent production may represent a type of bargain that is consistent with psychological and cultural evidence. A series of experiments in psychology and economics has found empirical support for the notion that labor inputs affect distributional decisions (Güth 1994; Königstein 2000; Selten 1978). In contrast to many economics experiments, which examine only 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, a number of experiments have also shown that concerns over fairness affect people's emotions, attitudes, and behavior toward 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 deemphasize score-keeping in social relationships in favor of 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 longer-term social relationships emphasized in cultural norms.

Table 4. Time-Delayed Contingency Estimates for Ache

Resource Type	kg-kg	%-%	ln(kg)-ln(kg)	sqrt(kg)-sqrt(kg)	frequency-frequency
Forest	0.008	0.051	0.023	0.030	0.050*
Cultigens	0.057*	0.145***	0.112**	0.136***	0.224***
Store-bought	0.001	0.157***	0.029	0.043*	0.053
All	0.095**	0.081*	0.160***	0.188***	0.261***

*** $p < 0.0001$, ** $p < 0.001$, * $p < 0.05$

Note: Sample size is 276 for each analysis.

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 used for the Ache considered only 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 on treks has been described as unconditional, 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 in activities that increase the caloric return rate only 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, Hill, and Kaplan 2002; Hill 2002).

Although the majority of the diet consumed during foraging treks is high-risk game, 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. Because of 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 are 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).

No particular social contract will benefit everyone equally. For example, high producers may benefit only when sick or injured (Gurven et al. 2000a; 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 insurance may pay off only during difficult times, and so, on average, imbalances in quantities exchanged are likely. Imbalances are more prevalent

among close kin and neighbors, who are likely to be committed to engage and invest in long-term relationships. It remains to be seen whether the estimated levels of contingency are sufficient to motivate high levels of production or other incentives are necessary. High producers may gain if high production acts as an honest signal of phenotypic quality, leading to greater mating opportunities (Smith and Bliege Bird 2000), or of cooperative intent or commitment (Frank 1988; Gintis, Smith, and Bowles 2001; Gurven et al. 2000a). Additionally, high producers may be able to trade surplus resources directly for other goods or services. Thus, other mechanisms may encourage higher levels of production than warranted by contingency alone.

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 make competing demands on individuals' production. Although ecological arguments have been made about the role of intra- and interforager variance in favor of more or less sharing (e.g., Winterhalder 1986), the determinants of such variation, apart from stochastic factors, have not been explored. Differential use of time, skill, and knowledge and intent are some of these determinants. 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.

Much ethnographic evidence suggests that expected patterns of distribution are linked to production in a structured way. Resource flows are linked to both the production of food and 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. Dependence on quantity or value may even be favored among foragers relying on unpredictable resources if group size is large enough to make the monitoring of labor inputs 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 strong interdependence, “fair” distribution norms should be based on the labor contributions of their members.

Acknowledgments

I thank the Ache of Arroyo Bandera and the Hiwi of Mahe-nemuthu for their kindness and support. I also thank Ray Hames, Eric Smith, Bruce Winterhalder, and two anonymous reviewers for their useful comments and suggestions.

References Cited

- Axelrod, R., and W. Hamilton. 1981. The evolution of cooperation. *Science* 211:1390–96.
- Bird, R. 1999. Cooperation and conflict: The behavioral ecology of the sexual division of labor. *Evolutionary Anthropology* 8:65–75.
- Bliege Bird, R. L., D. W. Bird, G. Kushnick, and E. A. Smith. 2002. Risk and reciprocity in Meriam food sharing. *Evolution and Human Behavior* 23:297–321.
- Blurton Jones, N. 1987. Tolerated theft: Suggestions about the ecology and evolution of sharing, hoarding, and scrounging. *Social Science Information* 26:31–54.
- Boyd, R. 1990. The evolution of reciprocity when conditions vary. In *Coalitions and alliances in humans and other animals*, ed. A. H. Harcourt and F. B. M. de Waal, 473–89. New York: Oxford University Press.
- Brosnan, S. F., and F. B. M. de Waal. 2002. Proximate perspective on reciprocal altruism. *Human Nature* 13:129–52.
- Cosmides, L., and J. Tooby. 1992. Cognitive adaptations for social exchange. In *The adapted mind: Evolutionary psychology and the generation of culture*, ed. J. Barkow, L. Cosmides, and J. Tooby, 163–228. New York: Oxford University Press.
- Fehr, E., and S. Gächter. 2002. Altruistic punishment in humans. *Nature* 415:137–40.
- Fehr, E., and K. M. Schmidt. 1999. A theory of fairness, competition, and cooperation. *Quarterly Journal of Economics* 114:817–68.
- Frank, R. 1988. *Passions within reason*. New York: Norton.
- Gintis, H., E. A. Smith, and S. Bowles. 2001. Costly signaling and cooperation. *Journal of Theoretical Biology* 213:103–19.
- Gurven, M. 2004a. Reciprocal altruism and food sharing decisions among Hiwi and Ache hunter-gatherers. *Behavioral Ecology and Sociobiology* 56:366–80.
- . 2004b. To give and to give not: The behavioral ecology of human food transfers. *Behavioral and Brain Sciences* 27:543–83.
- Gurven, M., W. Allen-Arave, K. Hill, and M. Hurtado. 2000a. “It’s a Wonderful Life”: Signaling generosity among the Ache of Paraguay. *Evolution and Human Behavior* 21:263–82.
- . 2001. Reservation food sharing among the Ache of Paraguay. *Human Nature* 12:273–98.
- Gurven, M., K. Hill, and H. Kaplan. 2002. From forest to reservation: Transitions in food sharing behavior among the Ache of Paraguay. *Journal of Anthropological Research* 58:93–120.
- Gurven, M., K. Hill, H. Kaplan, M. Hurtado, and B. Lyles. 2000b. Food transfers among Hiwi foragers of Venezuela: Tests of reciprocity. *Human Ecology* 28:171–218.
- Güth, W. 1994. Distributive justice: A behavioral theory and empirical evidence. In *Essays on economic psychology*, ed. W. G. H. Brandstätter, 153–76. Berlin: Springer.
- Hames, R. 1987a. Garden labor exchange among the Ye’Kwana. *Ethology and Sociobiology* 8:354–92.
- . 1987b. Relatedness and garden labor exchange among the Ye’Kwana: A preliminary analysis. *Ethology and Sociobiology* 8:259–84.
- . 2000. Reciprocal altruism in Yanomamo food exchange. In *Human behavior and adaptation: An anthropological perspective*, ed. N. Chagnon, L. Cronk, and W. Irons. New York: Aldine de Gruyter.
- Hawkes, K. 1993. Why hunter-gatherers work: An ancient version of the problem of public goods. *Current Anthropology* 32:341–61.
- Hawkes, K., J. F. O’Connell, and N. Blurton Jones. 2001. Hadza meat sharing. *Evolution and Human Behavior* 22:113–42.
- Hill, K. 2002. Cooperative food acquisition by Ache foragers. *Human Nature* 13:105–28.
- Hill, K., and H. Kaplan. 1993. On why male foragers hunt and share food. *Current Anthropology* 34:701–10.
- Hoffman, E., K. A. McCabe, and V. L. Smith. 1998. Behavioral foundations of reciprocity: Experimental economics and evolutionary psychology. *Economic Inquiry* 36:335–52.
- Königstein, M. 2000. *Equity, efficiency, and evolutionary stability in bargaining games with joint production*. (Lecture Notes in Economics and Mathematical Systems 483.) Berlin: Springer.
- Nöe, R., C. van Schaik, and J. van Hooff. 1991. The market effect: An explanation for pay-off asymmetries among collaborating animals. *Ethology and Sociobiology* 87:97–118.
- Rose, L. M. 1997. Vertebrate predation and food-sharing in *Cebus* and *Pan*. *International Journal of Primatology* 18:727–65.
- Selten, R. 1978. The equity principle in economic behavior. In *Decision theory and social ethics: Issues in social choice*, ed. W. L. H. Gottinger, 289–301. Dordrecht: Reidel.
- Smith, E. A., and R. L. Bliege Bird. 2000. Costly signaling and turtle hunting. *Evolution and Human Behavior* 21:245–61.
- Sugiyama, L., and R. Chacon. 2000. Effects of illness and injury on foraging among the Yora and Shiwiar: Pathology risk as adaptive problem. In *Adaptation and human behavior: An anthropological perspective*, ed. L. Cronk, N. Chagnon, and W. Irons, 371–95. Hawthorne, N.Y.: Aldine de Gruyter.

Winterhalder, B. 1986. Diet choice, risk, and food sharing in a stochastic environment. *Journal of Anthropological Archaeology* 5:369–92.

———. 1996. A marginal model of tolerated theft. *Ethology*

and Sociobiology 17:37–53.

———. 1997. Social foraging and the behavioral ecology of intragroup resource transfers. *Evolutionary Anthropology* 5: 46–57.