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To give and to give not: The behavioral ecology of human food transfers

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Abstract: The transfer of food among group members is a ubiquitous feature of small-scale forager and forager-agricultural populations. The uniqueness of pervasive sharing among humans, especially among unrelated individuals, has led researchers to evaluate numerous hypotheses about the adaptive functions and patterns of sharing in different ecologies. This article attempts to organize available cross-cultural evidence pertaining to several contentious evolutionary models: kin selection, reciprocal altruism, tolerated scrounging, and costly signaling. Debates about the relevance of these models focus primarily on the extent to which individuals exert control over the distribution of foods they acquire, and the extent to which donors receive food or other fitness-enhancing benefits in return for shares given away. Each model can explain some of the variance in sharing patterns within groups, and so generalizations that ignore or deny the importance of any one model may be misleading. Careful multivariate analyses and cross-cultural comparisons of food transfer patterns are therefore necessary tools for assessing aspects of the sexual division of labor, human life history evolution, and the evolution of the family. This article also introduces a framework for better understanding variation in sharing behavior across small-scale traditional societies. I discuss the importance of resource ecology and the degree of coordination in acquisition activities as a key feature that influences sharing behavior.

Keywords: behavioral ecology; cooperation; costly signaling; food sharing; foragers; reciprocal altruism

1. Introduction

Why do individuals give valuable resources away to others? To give or not to give is a special case of a more general dilemma: Why do individuals engage in acts that incur personal costs and benefit others? Behavioral researchers are interested in discovering both the "ultimate" level evolutionary explanations for observed patterns of resource transfer across societies (Winterhalder 1996b) and the "proximate" determinants that shape these and other costly prosocial behaviors (Caporael et al. 1989). Anthropologists have focused on explaining the pattern of food transfer among small-scale subsistence economies. Psychologists and economists have tried to understand the motivations for altruistic, "other-regarding" behavior in wetern societies with market economies (e.g., Andreoni 2001; Camerer & Thaler 1995; Rose-Ackerman 1996). Behavioral biologists have studied several prosocial behaviors including food transfer (e.g., capuchin monkeys, chimpanzees, vampire bats), grooming (e.g., impala, chimpanzees, baboons), foraging (e.g., lions, African wild dogs, killer whales), and group defense. Costly prosocial behavior is viewed by many of these researchers as "anomalous" (Dawes & Thaler 1990), because any behavior benefiting others at a substantial personal expense violates the "axiom of rationality" which assumes that higher levels of consumption provide higher individual utility.

One important source of information for understanding the evolution of prosocial behavior and cooperation is the rich literature on food transfers among people who meet their daily food needs from consuming wild foods and cultigens, with little access to modern markets. These are hunter-gatherers and small-scale forager-agriculturalists. The literature on food transfers among peoples practicing a subsistence economy has grown in the past twenty years. These data are useful for illustrating existing variation in cooperative sharing within and among groups, and may serve as a basis for systematic hypothesis testing.

Research among these groups is critical to resolve debates on the nature of human sociality and cooperation. First, evolutionary psychology emphasizes that the tendency for humans to cooperate, even among strangers in mock scenarios, experiments, and in real life, may be hardwired as a result of a long evolutionary history of cooperative big-game hunting and food sharing (e.g., Cosmides &

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Tooby 1992; Hill 2002; Hoffman et al. 1998). Common notions of fairness, equity, and punishment in many domains may have thus been shaped in the sharing context of a hunting and gathering lifestyle (Fehr & Schmidt 1999; Gintis 2000). These researchers should be concerned whether assumptions made about hunter-gatherers are well-founded and whether empirical results based on western, market-oriented groups are generalizable to a nonmarket, nonwestern context.

Second, economists attempting to revise standard economic theory to accommodate the results of numerous experiments among members of modern, western populations (e.g., Bolton 1991; Fehr & Schmidt 1999; Rabin 1993) could also benefit from a better understanding of the natural history of giving in traditional societies. The recent results of these same economics experiments played in nonwestern, nonmarket oriented settings, in conjunction with ethnographic observations, may indeed impact the way economists think about *Homo economicus* (Henrich et al. 2001b), and the extent to which markets may change norms of fairness and cooperative outcomes. Third, careful study of the variation in giving across ecological and social contexts among different individuals in nonmarket societies might also help psychologists and economists frame questions about the origins and functions of social preferences and such emotions as guilt, shame, jealousy, and pride, and help political scientists better understand people's attitudes towards contributing to the public good by paying taxes and through welfare reform (see Bowles & Gintis 1998; Roemer 1996).

Fourth, if the economies of scale and the high levels of specialization found in complex societies were made possible by the development of a prosocial brain developed during a long evolutionary history of hunting and gathering, then understanding the flexibility of "prosocial" behavior may help increase our understanding of how humans have succeeded in generating cultural institutions favoring cooperative outcomes, and subsequently populating the globe. Indeed, it has been suggested that the ability to reap gains from cooperation may be responsible for the recent proliferation of *Homo sapiens sapiens* (Boyd & Richerson n.d.) at the expense of earlier hominid forms.

Lastly, reinterpretations of men's hunting and sharing practices as mating rather than as subsistence "strategies," have called into question traditional notions of the sexual division of labor and the origins of the family (Bird 1999; Hawkes 1993). The extent to which men's food production and distribution strategies function as forms of family provisioning or as status display has repercussions on future depictions of the evolution of long-term pair bonds (i.e., marriage) and whether the nuclear family is best viewed as a cooperative or competitive enterprise. Whether men are an important source of calories for subsidizing women's reproduction and child growth within the family can also influence our understanding of the evolution of fundamental human life history traits, such as delayed childhood, long post-menopausal lifespans, and large brains (Hawkes et al. 1998; Kaplan et al. 2000).

Despite the growing realization that cooperation among hunter-gatherers is critical to resolving the important issues just mentioned, only a handful of ethnographic studies focus on food transfers, and few of these are systematic or quantitative, making cross-cultural comparison difficult (see sect. 4). However, references to food sharing and production in numerous ethnographies can be useful for highlighting observations that are inconsistent with particular hypotheses.

The goal of this article is to synthesize what is known cross-culturally about within-group food transfers among foragers and forager-agriculturalists in light of current theory. A complete behavioral ecology of food transfers should explain the function or purpose for food transfers in the first place, as well as examine the social mechanisms responsible for maintaining different levels of food transfers within populations. It should also predict quantitative aspects of sharing, based on social context, local conditions, and features of resource ecology. Food sharing, for example, has been explicitly modeled as an efficient means of reducing the high daily variance in acquisition (Kaplan & Hill 1985; Smith 1988; Winterhalder 1986). Others have suggested a social purpose for food sharing, in which giving acts as an honest signal of donor quality or intent (Gurven et al. 2000a; Smith & Bleige Bird 2000a; Zahavi & Zahavi 1997). Because most developed models propose specific benefits to food sharing, we also require a way to specify the relative importance of each hypothetical benefit to observed patterns of food transfers.

Several theoretical models may explain trends in within-group transfers. The most prominent of these include kin selection (KS), reciprocal altruism (RA), tolerated scrounging (TS), and costly signaling (CS) (see Winterhalder 1996b). Recent analyses of food sharing have led researchers to believe that several or all of these models might explain some of the variation within the same population (Gurven et al. 2000b; Hill & Kaplan 1993; Winterhalder 1996b). Efforts in the past fifteen years have focused on testing alternative hypotheses that can distinguish between these models. To date, most sharing studies have focused on one or only a few populations. Answers to several key questions can potentially resolve important issues about the general applicability of these models to food sharing in nonmarket settings. These include: (1) Is (large) game a public good? Do acquirers have control over the distribution of kills? (2) Is food transferred consistently from "haves" to "have-nots"? (3) Is giving food contingent on prior or expected future receiving? I survey available evidence on these topics, putting to rest the notion that any one model can easily explain hunter-gatherer food exchange. I argue that available evidence cannot rule out reciprocal altruism as an important determinant of most food transfers, nor can it entirely eliminate tolerated scrounging as an explanation of some food transfers. Nonetheless, scenarios of human life history, the sexual division of labor, and the evolution of the family that depend on a tolerated scrounging-based explanation for food sharing are on shaky ground because of the large number of observations that contradict predictions from that model. Costly signaling of genetic or phenotypic quality may also be a relevant yet narrow influence on the production and distribution decisions of certain age and sex classes of individuals. However, many instances of food transfers seem designed to signal a willingness to cooperate, which suggests that some form of reciprocity may be the major component of food sharing behavior.

Cross-cultural analyses of sharing require a standard vocabulary for talking about sharing in different populations. Gurven et al. (2001) introduce four terms that describe different aspects of sharing. Sharing *depth* refers to the percentage of food production given to members of other nu-

clear families (e.g., 77% of all fish obtained is given to other families). *Breadth* is the number of other individuals or different families who receive from a given distribution, or alternatively, over a given sample period (e.g., on average 4.3 families receive a portion from each deer killed).[1] *Equality* reflects any disparities in amounts given to different individuals or families in the population (e.g., family *B* received 6.7% of the food produced by family *A,* but family *C* received only 1.2% of *A*'s total food production). *Balance* describes long-term differences in amounts transferred between pairs of individuals or families (e.g., family *A* gave 47 kg of meat but received back only 12 kg of meat from family *B* over a 3-month observation period). Each of these measures describes a separate domain of giving or receiving. These four measures allow detailed comparisons of sharing behavior within and across groups, and can therefore facilitate intracultural and cross-cultural hypothesis testing.

In this article, I discuss transfers of all food types.[2] Early observations of extensive meat sharing among social carnivores, the absence of sharing among herbivores and frugivores (Price 1975), and the popularized role of hunting in hominid social evolution (Washburn & Lancaster 1968) have led to a biased focus on game distributions in the sharing literature. Transfers of gathered foods and other food items are either rarely mentioned in ethnographies and food sharing studies, or given only minimal treatment. Even when strong evidence suggests that transfers of game may be explained by a single model, as in the sharing of sea turtles among the Meriam according to tolerated scrounging (Bliege Bird & Bird 1997), identical patterns cannot be inferred for all other components of the diet. If the Meriam reciprocally share yams, bananas, and chicken, or if the Hadza reciprocally share roots and small game – foods which contribute significant calories to the diet – then the fact that large game may be shared according to tolerated scrounging in these societies tells only part of the story of forager food sharing.

2. Models of food sharing

Imagine a male forager with a fresh kill, or a female forager with a basket of fruits or roots. Each must decide (or have decided for them): (1) How much to give to others (depth); (2) How many families should receive a share (breadth), and (3) How much should be given to each of *n* other locally available individuals (equality)? Each model discussed gives *ceteris paribus* conditions that predict when sharing should occur. These differ in the kinds of benefits returned to donors, and the manner in which these benefits are paid.

2.1. Kin selection-based nepotism (KS)

Because biological kin have a higher probability of sharing identical alleles by descent, kin-selected food sharing should favor biased transfers toward kin. The conditions which favor kin-selected sharing can be defined by a simple version of Hamilton's rule (Hamilton 1964), as $rB > C$. An individual should give to kin when the benefits, *B,* to a recipient, weighted by Wright's coefficient of relatedness, *r,* outweigh costs, *C,* to the donor.[3] *B* and *C* should be measured as impacts on survival and fertility, although these parameters have not been measured in any food sharing study among humans, and in only several cases among other organisms (Wilkinson 1988). It is important to remember that merely showing that kin receive food does not demonstrate nepotism, especially when the majority of one's neighbors and peers may be related by some degree to any acquirer. A weak test of nepotism predicts that kin should at least receive more than nonkin, and close kin ($r = 0.5$, offspring, parents) should receive more than distant kin ($r = 0.25$, grandparents, grandchildren, $r = 0.125$, first cousins). A stronger test must show that a kin bias is not just a result of reciprocal altruism or tolerated scrounging.[4]

2.2. Reciprocal altruism (RA)

One may also give portions of food to individuals with whom one has shared in the past, and from whom one is likely to receive shares in the future. The critical aspect of RA is that potential receipt in the future is an incentive for giving in the present (Trivers 1971). This is the concept of contingency (de Waal 1997a; 1997b; Gurven et al. 2000b; Hames 2000). Although tit-for-tat, as modeled via an iterated Prisoner's Dilemma (Axelrod & Hamilton 1981), is often equated with RA in the game theory literature, tit-for-tat is only one manifestation of RA (e.g., see Nowak & Sigmund 1990). A donor who gives a share to an unrelated individual may not know when he may receive a share in return, nor how much he is likely to receive, but may nonetheless give the morsel away, as long as time-discounted expected returns outweigh the costs of the initial sharing. RA, as well as KS and TS (sect. 2.3), are likely when *B* is significantly greater than *C*. Thus, the reciprocal transfer of unequal amounts of food is consistent with RA and expected from bargaining theory under a variety of conditions (see also Boyd 1992; Frean 1996). RA found in traditional societies may reflect a type of health insurance, where long-term benefits only sometimes outweigh the costs of giving (Gurven et al. 2000a).[5] Trade is a form of RA in which the products given and received are in different currencies (Hill & Kaplan 1993). Thus, meat for sex, fish for carbohydrates, honey for social deference, and fruit for assistance in clearing a field are examples of trade. Although both trade and in-kind reciprocity yield net benefits to the donor, only in-kind reciprocity has the effect of risk- or variance-reduction in daily intake of specific food types (Hawkes 1993).

A related model called "strong reciprocity" (Fehr et al. 2002; Gintis 2000) states that high levels of sharing are supported by punishing or rewarding not only those who defect or cooperate with you in dyadic interactions, but those who defect or cooperate with others. This form of reciprocity has been invoked to explain cooperation with nonkin under one-shot and anonymous conditions, which is not easily explained by the other models discussed here. Cultural group selection models are invoked to explain how such a system could evolve. The ethnographic evidence distinguishing RA from strong reciprocity (i.e., instances of third party punishment) is thin, and so for this article I do not compare the two models, because both are still very different from the other models discussed in this paper.

2.3. Tolerated scrounging or theft (TS)

If individuals get smaller increments of value from consuming additional portions of food, then remaining food portions will eventually be worth more to hungry individuals than to the sated acquirer. When one is unable to main-

tain control of a resource without paying a substantial cost to defend "surplus" food, an acquirer should cede portions to other individuals if this price of defense is greater than the additional value that could be gained from consuming those extra pieces (Blurton Jones 1987). The acquirer should cede portions until all potential contenders have equal marginal consumption value or utility (Winterhalder 1996a). Thus, tolerated scrounging (TS) describes food flows from haves to have-nots, when food given away is not contingent on shares received. If a producer can control who receives and how much, or if marginal value is linear or increasing (as a result of trade, for example), then TS is unlikely to explain food transfers. As in RA, medium to large-sized items that are acquired intermittently are most susceptible to sharing by TS.

2.4. Costly signaling (CS)

The food quest often involves tasks that require great risk, skill, stamina, and vigor. If success in these tasks is a result of certain valued characteristics of the acquirer, then engaging in those tasks may represent an honest signal of phenotypic quality. They are honest because they are not easily faked, and they can therefore provide reliable information about some quality of the acquirer. Although less explored, sharing can also be an honest signal of intent, either to initiate or maintain cooperative relations with other individuals. Signaling used as advertising for partner choice in social endeavors is relevant when RA is important (Alexander 1987; Frank 1988; Gurven et al. 2000a). It is therefore important to separate costly signaling (CS) of quality versus intent.

CS of phenotypic quality is similar to Hawkes' (1991; 1992) show-off hypothesis, which argues that men target risky game items because of social or mating, rather than consumptive, benefits, but differs in two important ways. First, it does not require TS-based sharing. It therefore does not assume that sharing is determined only by resource package size and asynchronicity in acquisition. Second, CS avoids the second-order collective action problem of who should reward generous sharers, because those that choose sharers as mates, allies, or other social partners, do so as a response to the advertised qualities of those individuals, and *not* as a form of payback for transferred food or as an encouragement for the good provider to stay with the social group (Smith & Bliege Bird 2000a). Thus, donors should not resent a lack of giving on behalf of past recipients, nor should recipients feel obliged to return benefits to a donor. One might also expect marital conflicts over sharing decisions to the extent that men's and women's interests converge. Applications of the show-off hypothesis have only been invoked to explain *men*'s foraging and sharing decisions, and with respect to large game, because of the proposed mating benefits accorded high status, even though signaling benefits may also include alliance building, social support, and mating opportunities for offspring. It is not invoked to explain food transfers by men of other resources (e.g., fruits, roots, honey, firewood) nor of food transfers by women.

3. Predictions of sharing models

The relevance of these models with respect to any particular society is difficult to assess because many predictions are consistent with several of the models. An analysis of the specific costs and benefits of sharing necessary to compare the impact of each model would require a level of estimation unseen in existing quantitative analyses. For this article, I focus on several key predictions that are most useful for distinguishing among the four models:

3.1. Producer control

An assumption of TS is that producers have little to no control over who receives shares of items they acquire because these items are relinquished to those with greater need. TS asserts that only relative need and power should have any influence on the direction of food transfer. Without producer control, any agent-centered model that tries to understand directed transfers as a function of individual payoffs is suspect, unless the "goals" of the appropriate decision-maker(s) correspond with those of the acquirer. Thus, lack of producer control over redistribution is inconsistent with KS and RA, but is consistent with CS.

3.2. Need

The principal determinant of food flows in TS is the need of potential recipients relative to that of the acquirer. Assuming equal ability to defend resources (resource holding potential), food portions should flow to recipients until all possess the same marginal value of consumption (Winterhalder 1996a). TS therefore directs food flows from haves to the have-nots, and in the simplest scenario (i.e., no differential information or travel costs, equal marginal values for additional portions), egalitarian distributions among all recipients (including the acquirer) are expected. Any strong bias in food sharing – towards kin (KS), neighbors, specific individuals (RA), and so forth – is therefore inconsistent with this assumption, unless these preferred recipients show greater relative need than other potential recipients or can obtain benefits at a smaller cost (e.g., smaller traveling or monitoring costs). According to CS, we should also not find biased transfers toward privileged others based on need, because the payoffs to signaling derive only from the honest display of production to a wide audience, and not from giving to specific individuals.

3.3. Contingency

Only RA requires that food be given on condition of expected future receipt. Producers giving more to specific people should receive more back from those people, and similarly, those who do not give should not receive. This requires some form of punishment or ostracism of "defectors." If shares are returned in the future, the net present value of expected future shares should at least compensate for the present costs of giving. As mentioned, a contingency effect is generally inconsistent with TS.[6] Although CS does not require contingency among specific pairs of individuals, someone, perhaps other than the recipients, is required to provide a benefit to offset the costs of giving up food to signal quality. Thus, according to CS, donors should not be angry or upset if recipients do not return favors, nor should recipients feel obligated to return those favors. It is important to emphasize that CS requires a generalized payback from others, whereas only RA requires a payback from past recipients. KS provides automatic benefits through in-

creased inclusive fitness, whereas TS avoids a cost and thus provides no benefit.

Much theoretical work and ethnographic discussion on sharing has focused on function – reducing the risk of daily food shortfalls or reducing intake variance resulting from variance in acquisition (Smith 1988; Winterhalder 1986). It is important to realize that RA, TS, KS, and CS can all produce these effects; thus demonstrating that group-level benefits from food sharing practices is not revealing.

The importance of surveying what is known about foragers in relation to these individual-oriented models has become evident in light of the issues raised in the beginning of this article, particularly the recent arguments over men's foraging goals (Hawkes 1993; Hill & Kaplan 1993), the sexual division of labor (Bird 1999), and the evolution of a human life history (Hawkes et al. 1998; Kaplan et al. 2000). If foragers lack producer control and if nothing is given in return for that which is received, then the production of large, asynchronously acquired resources (i.e., wild game or any moderately large, valuable resource) is a partial public good, because others cannot be excluded from receiving shares. Food production, or allocation to the public good, is thus viewed as a collective action problem because nonproducers consume portions without paying any production costs. Without producer control and contingency, the traditional notion of hunting as a family provisioning strategy is therefore suspect. It is then argued that men hunt and share game widely as a form of mating effort, vis à vis the show-off hypothesis and CS of phenotypic quality.

4. The cross-cultural record

Table 1 lists all the hunter-gatherer and forager-agriculturalist groups for which I was able to find explicit quantitative or qualitative descriptions of food transfer patterns. Quantitative studies are in italics. Of the 45 groups listed, 27% are from South America, 23% from Africa, and the remain-

Table 1. *Worldwide ethnographic sample*

Hunter-Gatherers (33)

Africa
Hadza (Hawkes et al. 1991; 2001; Marlowe n.d.)
Kutse Basarwa (Kent 1993)
Dobe !Kung (Lee 1972; 1979)
G/wi Bushmen (Silberbauer 1981; Tanaka 1980)
Nyae Nyae !Kung (Marshall 1976)
Efe Pygmies (Bailey 1991)
Aka Pygmies (Bahuchet 1990; Kitanishi 1996; 1998)
Mbuti Pygmies (Harako 1976; Ichikawa 1981; 1983)

South America
Pilaga (Henry 1951)
Yora/Yaminahua (Hill & Kaplan 1989)
Ache (Kaplan et al. 1984; 1985)
Siriono (Holmberg 1969)
Hiwi (Gurven et al. 2000b)
Kaingang (Henry 1941)
Ayoreo (Bugos & McCarthy 1984)
Lengua (Grubb 1911)

North America
Dogrib (Helm 1972)
Central Eskimo (Balikci 1970; Damas 1972)
Mistassini Cree (Rogers 1972)
Washo (Price 1975)
Tolowa (Gould 1981)
Tututni (Gould 1981)
Coast Yurok (Gould 1981)
Shoshone (Fowler 1986; Steward 1938)
Inujjuamiut (Smith 1991)

Australia
Gunwinggu (Altman 1987)
W. Desert Aborig. (Gould 1981; Myers 1988)
Yolngu (Peterson 1993)
Pintupi (Myers 1988)

Southeast Asia
Agta (Griffin 1982; Peterson 1978)
Lamalera (Alvard 2002; Alvard & Nolin 2002)
Batek (Semang) (Endicott 1988)
Onge (Bose 1964)

Forager-Agriculturalists (13)

South America
Maimande (Aspelin 1979)
Yanomamo (Hames 1990; 2000)
Yuqui (Stearman 1989)
Ache (Gurven et al. 2000a; 2001; 2002)
Chácobo (Prost 1983)

Africa
Basarwa Kung (Cashdan 1985)
Tswana/Kalanga (Cashdan 1985)

Islands
Ifaluk (Betzig 1988; Betzig & Turke 1986; Sosis 2000a; 2001; Sosis et al. 1998)
Meriam (Bliege Bird & Bird 1997; Bliege Bird et al. 2002)
Batak (Cadelina 1982)
Kubo (Dwyer & Minnegal 1991; 1993)
Fanalei (Takekawa 1996)
Maori (Firth 1929)

Italicized terms signify quantitative studies.

ing are from Australia, North America, and Southeast Asia. Although these percentages may not accurately reflect the worldwide representation of foragers and small-scale nonmarket economies, this list includes all available studies that I could find in the literature. Information on each topic discussed was not available for all groups listed in Table 1, and so omission of a group for a specific topic does not necessarily imply an absence of that behavior in the group. Undoubtedly, other ethnographies with scant mention of sharing-related information are not included in this article. Nonetheless, a large number of cases are drawn upon to examine whether the weight of evidence is unidirectional with respect to the inquiries and predictions made at the beginning of this article.

4.1. Do producers have control over distributions?

Descriptions of widespread sharing where everyone present in camp sometimes receives portions of a kill (e.g., Western Desert Aborigines, Ache, G/wi, Kubo), where kills are handed over and butchered by individuals other than the hunter (e.g., Ache, Efe Pygmies, Gunwinggu, Ona), where specific cultural rules delineate which classes of individuals receive specific portions of game animals (e.g., Copper Eskimo, Aka Pygmies, Lamalera, Gunwinggu, and Western Desert Aborigines), or where hunters receive no more than other band members (Ache, Batak), have led some investigators to conclude that hunters exert little influence over the distribution of game (Bird 1999; Dowling 1968; Hawkes 1993). Without producer control, the question "Why bother hunting if the spoils go to other people?" is a legitimate concern, because food may then be viewed as a public good. As argued earlier, if exclusions are possible because of a moderate level of producer control over the character of distributions, then game is not a public good. Observing the extent of producer control is confounded by a lack of understanding of how distribution decisions are made in the context of the conflicting push and pull of interested parties. It is also confounded by the implicit assumptions that lack of control is signified by a hunter's receiving $1/n$, and that complete control is viewed as an ability to hoard 100% of a resource. However, keeping $1/n$ does not signify a lack of control if the acquirer decides that $1/n$ is the optimal portion to keep, given the expected payoffs from sharing. Even when hunters relinquish complete control of game, as among the Ache, such abandonment may be voluntary, as Ache do not relinquish control when at the reservation (Gurven et al. 2002).

Producer control of distribution is indicated by several common ethnographic distribution patterns. Many studies report biased distributions, preferential shares to acquirers and their families, or more frequent sharing to close kin outside the nuclear family at the expense of more distant kin and unrelated individuals (Gunwinggu [Altman 1987], Copper and Netsilik Eskimo [Damas 1972], Pilaga [Henry 1951], Hiwi [Gurven et al. 2000b], Kaingang [Henry 1941], Batek [Endicott 1988], Pintupi [Myers 1988], Washo [Price 1975], Yanomamo [Hames 1990], Basarwa [Cashdan 1985], Ifaluk [Sosis 2001; Sosis et al. 1998], Agta [Griffin 1982], Ache [at reservation] [Gurven et al. 2001], Machiguenga [Kaplan, personal communication], Tsimane [my own observation]). Although it is possible that close kin may be more likely to live in closer proximity than other individuals (and hence are more likely to demand shares), the few studies that examine both kinship and distance reveal that close kin receive more than other individuals, even when controlling for residential distance (Hiwi [Gurven et al. 2000b], Ache [at settlement] [Gurven et al. 2001]). An additional bias common in many forager societies is the bride service tradition, whereby young men must provide meat for their new wife and in-laws (!Kung [Leacock 1982]; Yanomamo [Ritchie 1996]; Hadza [Woodburn 1998]).

Expectations of sharing are usually greatest in camp, which leaves the option for some hunters to consume small portions of their catch at or near the kill site prior to transporting it back to a communal camp. Indeed, hunters are rarely criticized by others if they consume internal organs and marrow from game at the kill site (e.g., the !Kung [Speth 1990], the G/wi [Silberbauer 1981], the Nyae Nyae !Kung [Marshall 1976], the Hadza [Woodburn 1998], and the Batek, where "no one begrudges them this right" [Endicott 1988, p. 117]). Several Lengua men gorged themselves full of ostrich eggs, returning to camp with only a few, so that they wouldn't have to share with those who were not producing enough (Grubb 1911, p. 190). Ache hunters, for example, could potentially bring family members directly to the kill site to cook and consume meat, but this never happens. In all of these groups, much food is transported to camp, an observation that is consistent with a desire to share food.[7]

A higher percentage of big game is distributed to more families than small game in all groups in which the effect of resource package size has been examined (Hiwi [Gurven et al. 2000b], Ache [Kaplan & Hill 1985; Gurven et al. 2001], Dobe !Kung [Lee 1979], Kutse [Kent 1993], Yanomamo [Hames 1990], G/wi [Silberbauer 1981], Nyae Nyae !Kung [Marshall 1976], Ifaluk [Sosis et al. 1998], Aka [Kitanishi 1998], Fanalei [Takekawa 1996]), which suggests either greater opportunities for hunters to gain benefits through increased exchange (due in part to diminishing returns to hoarding for the acquirer) or that producers have increasingly less control over distributions. Even if greater sharing depth and breadth were indicative of declining producer control, producers often receive significantly more than $1/n$, thereby making the production of large resource packages worthwhile. During one season in 1987, a Gunwinggu family composed only 20% of the band, provided 41% of the band's total calories, and kept twice as much as the other household cluster (Altman 1987). Similarly, Hiwi and Ache families represented 3% and 5% of their village settlement populations in 1990 and 1998, and kept 20% or more of what they acquired, including meat, giving the rest to fewer than six other nuclear families (out of 23 and 36, respectively) (Gurven et al. 2000a; 2000b). Although Yora families divide game equally on forest trips, they kept about 40% of acquired game at the village settlement, giving the rest to three (out of ten) other families (Hill & Kaplan 1989). About 69% of acquired meat was kept within the family of Yuqui hunters, with the rest given to about five other hunters out of fifteen (Stearman 1989). Yanomamo hunters kept twice as much food for their families than was given to each other family (Hames 2000). Similarly, Hadza hunters' share of large game items are almost twice as large as those given to others (Hawkes et al. 2001).

If hunger gives others claim to shares, thereby reducing producer control, then it is unclear why smaller resource items are frequently kept within the nuclear family of the acquirer even though others may be hungry.[8] Small game,

such as steenbok, duikers, and tortoises, are frequently consumed within an acquirer's family among the Dobe !Kung (Lee 1972) or those "people close to the hunter" among the G/wi (Silberbauer 1981), even though the size of some of these small animals is comparable to those which are widely shared among other groups, such as the Ache. Thus, as reported among Western Desert Aborigines, even small game meat is distributed as tiny portions so that "everyone in camp gets a share" (Gould 1981:432).

Others' hunger levels should also increase during periods of food scarcity. According to TS, any increased demand for food should increase the breadth and/or depth of sharing, and according to CS, high levels of sharing should make effective signals of producer quality during lean periods. Case reports of the Ik (Turnbull 1972), the Ojibwa Indians (Bishop 1978), and the Northern Shoshone (Moulton & Dunlay 1983) however, demonstrate less sharing during stressful times. The Batak share with significantly fewer households during the preharvest season when food is scarce. The average geographical distance between sharing households during this time is about one-half the distance during more plentiful seasons (Cadelina 1982). Although risk-sensitive foragers, during periods of scarcity, may favor the risk-prone strategy of little or nosharing, the fact that across foragers, sharing breadth and depth does not increase while others' demand for food is very high, suggests adequate control over distributions.

Another common pattern among the subset of groups where men hunt cooperatively is for game to be distributed initially among all participants in the hunt (Netsilik Eskimo [Damas 1972], Nyae Nyae !Kung [Marshall 1976], NW Coast Indians [Gould 1981], Ifaluk [Sosis 2000a; 2001], Pintupi [Myers 1988], Washo [Price 1975], Mbuti [Ichikawa 1983], Aka [Kitanishi 1996; 1998], Efe [Bailey 1991], Shoshone and Paiute [Fowler 1986], Lamalera [Alvard 2002], Hiwi [Hill, personal communication]). Several ethnographies are explicit about subsequent exclusive ownership of meat shares upon initial receipt in a primary distribution, regardless of whether or not others have received their own shares (Mbuti [Ichikawa 1983], Nyae Nyae !Kung [Marshall 1976], Kaingang [Henry 1941], Efe [Bailey 1991]). This is exemplified by Marshall's statement about the Nyae Nyae !Kung that "when an individual receives a portion of meat, he owns it outright for himself. He may give and share it further as he wishes, but it never becomes family or group property" (1976, p. 363). Similarly, Bailey writes that although cooperatively acquired game is shared among Efe hunters, meat acquired by solitary hunters is "entirely his to allocate as he pleases" (Bailey 1991, p. 100).

Although frequent protestations often make distributions the subject of strife, the occurrence of demand sharing (Peterson 1993; Woodburn 1998) does not imply a lack of producer control due to high costs of defending resources. Henry (1951) reports that Pilaga families are able to bias food toward specific households despite the objections of other individuals. Among the Siriono, "one may be accused of hoarding food, but the other members of the extended family can do little about it except to go out and look for their own" (Holmberg 1969, p. 88). People do not have automatic claim to others' acquisition among the Pintupi, where "sharing often takes place only on request" (Myers 1988). Aka Pygmies often do not share food, and "distribution within the camp is actually voluntary . . . the family chooses whether or not it shares its meals and with whom it shares . . . temporary disappointment is evident when a household is left out of a distribution" (Bahuchet 1990, p. 38). Although the Agta are reported to share most foods equally among available families, they often set aside separate portions of meat to be used in trading for carbohydrates with non-Agta neighbors (Griffin 1982).

4.2. Does food flow according to need?

Much has been written about the emphasis placed on generosity, and the "moral obligation" to help others in need among traditional societies (Barnard & Woodburn 1988), exemplified by the Chácobo proverb, "If you are a human being, then you will share what you have with those who are in need" (Prost 1983, p. 64). Marshall writes that among the Nyae Nyae !Kung "if there is hunger, it is commonly shared. There are no distinct haves and have-nots" (1976, p. 357). Although populations tend to vary over the extent of explicit praise of generosity, there is often mention of a direct condemnation of stinginess. "The most serious accusations one !Kung can level against another are the charge of stinginess and the charge of arrogance." (Lee 1979, p. 458). Similarly, one of the most serious Ache insults is to call somebody *mella* (a nongiver). The Yanomamo are "so preoccupied with the possessions (including food) of others . . . anyone who has more than a day's supply of anything is a potential target of an accusation of stinginess if he does not share" (Hames 1990, p. 103). Lengua who insist on keeping food for themselves are similarly "hated and terrorized by others" (Grubb 1911, p. 190). These descriptions support the view that social dynamics in small-scale societies are organized by an ethic of "assertive" or "fierce" egalitarianism (Boehm 1999; Woodburn 1982) and that "demand sharing" equalizes differences resulting from production ability. Because strong pooling norms reduce variance in benefits as well as costs, certain leveling mechanisms have been proposed as cultural means of limiting the arrogance and wealth accumulation of hunters (or anyone for that matter) (Dowling 1968; Wiessner 1996; Woodburn 1982). These include ridicule of a hunter's prowess (!Kung [Lee 1979]), taboos against hunters consuming portions of their own kills (e.g., Ache [Clastres 1972], Hadza [Woodburn 1982], and Ona [Bridges 1948]), and explicit sharing rules (e.g., Central Eskimo [Damas 1972], Gunwinggu [Altman 1987]). Additionally, it has often been stated that refusing to give shares to others upon request is "the ultimate sin" (Prost 1983, p. 52), and that even when food is not obligatorily indebted to others, requests for shares are rarely denied (e.g., Batek [Endicott 1988], Pintupi [Myers 1988], Kaingang [Henry 1941], Kutse [Kent 1993]).

These cultural notions manifest themselves in ways that encourage egalitarianism. Anecdotes of horticulture failing among the Hadza (Woodburn 1982), Batek (Endicott 1988), Hiwi (Hill, personal communication), and Agta (Headland 1986) resulting from incessant pressures on the hardest-working to give away the bulk of their production, are consistent with assertive egalitarianism. The fact that men still hunt even though some selfish benefits may be denied via various leveling mechanisms suggests that these hunters either retain additional portions (as argued earlier), gain other benefits through reciprocity or trade, or obtain mating or other benefits through costly signaling (but see sect. 5).[9]

Although norms regarding ideal distributions are preva-

lent cross-culturally, they do not necessarily eliminate producer control or producer advantage, nor do they indicate that givers do not gain any advantage by helping needy individuals. Cultural rules or expectations need not mesh with daily transactions (Pennington & Harpending 1993). Indeed, Altman and Peterson (1988) report that explicit sharing rules for dividing large macropods among the Gunwinggu account for only 50% of game items. Among the Aka, estimates of the percentage of different game items shared with other individuals differed substantially from the amounts predicted by sharing rules (Kitanishi 1998). Extensive descriptions of quarrels over food distributions among the !Kung, the Siriono, and the Yanomamo are also testament to the fact that rules do not always cleanly predict behavioral outcomes.

There is quantitative evidence that giving does indeed reflect the relative need of recipients. Among Ache (Gurven et al. 2001; Kaplan & Hill 1985), Maimande (Aspelin 1979), and Hiwi (Gurven et al. 2000), shares are given in proportion to the number of consumers within the recipient family. These observations are consistent with both TS and RA. Families with high dependency tend to be net consumers whereas those with low dependency are net producers among the Batak (Cadelina 1982). Among the G/wi, the largest shares of game are first given to families with dependent children, then to those without children, and the smallest shares are given to single individuals (Silberbauer 1981). There is also some description of younger Ache, Gunwinggu, Efe, Kutse, and Agta hunters ceding portions of game to older men who may bias distributions in their own favor, with the end result being that older hunters with more children (and hence greater caloric demand) benefit more from sharing than do the younger hunters with small or no families. Furthermore, prolific hunters often subsidize other band members, and often give away more than they receive back (Yuqui [Stearman 1989], Ache [Gurven et al. 2000a], Hiwi [Gurven et al. 2000b], Kutse [Kent 1993], Efe [Bailey 1991]). Even at a permanent Ache settlement where cultivated foods constitute the majority of the daily diet, higher producers give an increasingly higher proportion of their production away to members outside their nuclear family (unpublished data), consistent with the notion of a progressive tax on income (Woodburn 1982).

There is, however, little question that limitations on the kinds and amounts of benefits that accrue to good hunters exist, and that self-interest models which ignore constraints of group living will not completely explain variation in food sharing patterns. Group living implies a series of trade-offs where high producers may compromise their production in exchange for some other group-derived benefit, such as defense against enemies and predators, trade, and increased mating access. If individuals are free to move among bands or villages (except for transaction costs), then these group-derived benefits (and not risk-reduction) must influence the perceived costs and benefits of sharing decisions when donors give more than they receive (see Dwyer & Minnegal 1992). Empirical studies need to explore the possibility that consistently generous individuals may receive prestige, support, or social insurance (discussed in sect. 8.2), and that these social benefits have fitness consequences, before concluding that generous donors give according to TS. Giving (and producing) because of sanction-avoidance is a key feature of "strong reciprocity," which may also offer insight into the evolution of costly giving, as opposed to other costly displays of phenotypic quality (Fehr et al. 2002; Gintis 2000). Here, altruism is maintained by prosocial norms enforced by direct, indirect, and third-party punishment.

Although the preceding discussion shows that need is a salient component of sharing, need does not dictate the entire character of daily distributions. Necessity for food can be a result of differential abilities, knowledge, luck, or high dependency, and there is no reason to expect the same patterns of distribution for all four causes of need (see sect. 5). Furthermore, biases in distributions mentioned in the previous section, as well as the influence of proximate factors, such as population size and privacy, can all influence the salience of need in food transfer decisions.

Need also may not correlate with sharing outcomes when individuals differ in what is referred to by biologists as "resource holding potential" (RHP). RHP includes physical prowess, authority, social influence, or any ability that can allow an individual to defend resources more easily, or to extort resources from other less powerful individuals. According to TS, only powerful individuals can avoid relinquishing shares to hungry individuals. RHP has never been measured in any society, especially because any single factor, such as muscular strength, fighting ability, or age, may not accurately predict RHP. Many observations, however, are inconsistent with RHP-based predictions. People often save plates of food for absent individuals, even though other group members may not receive any portions. Hungry children often receive food from adults other than their parents. Village chiefs and influential individuals often give away more food than they receive.

4.3. Do donors get back more utility than they give away?

The notion that giving is conditional on expectations of future receiving (based perhaps on past receiving) is difficult to test. Sahlins's (1972) "generalized reciprocity" implies that in-flows and out-flows should balance over the course of people's lives, but that daily giving is done without reference to any accounting procedure. As pointed out by Hawkes (1992), this general anthropological description of reciprocity differs from the way RA is commonly used among biologists and evolutionary anthropologists. The maintenance of RA requires that beneficiaries give a return benefit back to the original donor. Several factors are crucial in determining how much is returned to pay back a donor: the cost to the donor of giving, the benefit to the recipient, the time delay into the future when a benefit is returned, and the benefit to the original donor of receiving in the future. A suitable condition for RA occurs when benefits to recipients greatly outweigh the costs to donors – precisely the need-based condition compatible with TS and KS. One problem with identifying and measuring contingency lies in the choice of an appropriate time frame over which reciprocation should occur (Gurven et al. 2000b; Hawkes 1992; 2000b). At which point is a lack of reciprocation considered a defection? Does giving back half of what one was given constitute an act of reciprocation or defection?

Economic bargaining theory offers an appropriate way for understanding contingency and RA (Gurven et al. 2000b; Hill & Kaplan 1993; Sosis et al. 1998; Ståhl 1972). Donors should give as long as the expected future benefit outweighs the current costs of giving relative to other op-

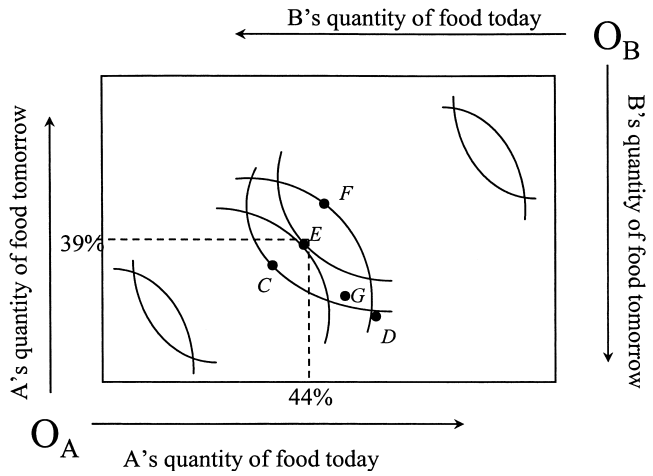

Figure 1. Edgeworth Box of Food Exchange. Curved lines are indifference curves describing the exchange between individuals *A* and *B* of their present and future acquisition. Point C lies on *A*'s indifference curve, point F on *B*'s indifference curve. The closed oval of overlapping indifference curves is the bargaining zone, whereas point E represents the intersection, or final bargain between individuals *A* and *B*. In this hypothetical scenario, *A* gives away 44% of his food today to *B* in exchange for 39% of *B*'s food tomorrow.

tions; thus, the exchange of unequal quantities is often consistent with RA. Figure 1 shows an Edgeworth box (Edgeworth 1881) representing the exchange of *A*'s present production for *B*'s future production. Concave curves radiating from the lower left and upper right corners represent the utility *A* and *B* derive from consuming some combination of *A*'s (or *B*'s) present and *B*'s (or *A*'s) future production. The oval region in the interior represents the "bargaining zone". *A* and *B* can both expect to gain if the final bargain is struck anywhere in this region, although they may not benefit equally. Where the final bargain is struck should be influenced by the relative bargaining power of the interactants, which reflects the expected cost from giving and benefit from receiving a specific quantity of food. These costs and benefits could vary with the amount of existing wealth, influence, production ability, status, or number of dependent offspring. Thus, exchange does not have to be perfectly balanced to be perceived as beneficial to involved parties and maintained by RA.

The proportion of receiving that is contingent on giving has been estimated in only eight groups, four of which are located in South America: the Hiwi (Gurven et al. 2000b), Ache (Gurven et al. 2000a), Yanomamo (Hames 2000), Pilaga (my analysis based on data from Henry 1951), Aka (my analysis based on data from Kitanishi 1998), Hadza (my analysis based on Appendix A, Hawkes et al. 2001), Meriam (Bliege Bird et al. 2002), and Dolgan/Nganasan (Ziker 2002b). Contingency is calculated as the correlation between the amount or percent of total production *A* gives *B* with the amount or percent *B* gives *A*, over a sample period which usually ranges from several weeks to several months.[10] Most correlations given in Table 2 are statistically significant and range from 0.16 to 0.65 when considering the exchange of any food item for any other food item. Limiting the foods to wild game, the range is 0.10 to 0.46, with no contingency found for Ache meat sharing on temporary

Table 2. *Measures of contingency*

	Correlation, *r*		
Group	All food	Meat	Source
1. Hiwi	0.18***	0.34***	Gurven et al. 2000b
2. Ache (forest)	0.26*	−0.16	Gurven et al. 2002
Ache (settlement)	0.36***	0.10*	Gurven et al. 2001
3. Yanomamo (1)	0.16*	—	Hames 2000
Yanomamo (2)	0.21*	—	Hames 2000
Yanomamo (3)	0.29*	—	Hames 2000
Yanomamo (4)	0.50*	—	Hames 2000
4. Pilaga	0.42*	—	Henry 1951
5. Aka	0.60**	0.44***	Kitanishi 1998
6. Hadza	—	0.46***	Hawkes et al. 2001
7. Meriam	0.14	0.01	Bliege Bird et al. 2002
8. Dolgan/Nganasan	0.65*		Ziker 2002b

***$p < 0.0001$, **$p < .0001$, *$p < 0.05$.
Note: Meriam meat refers to turtle meat exchanges only.

foraging trips out from a reservation settlement or Meriam turtle sharing (see sect. 8.2). Measurement error aside, these numbers suggest that an acquirer giving away 1% of his production can expect to receive only about 0.33% of a recipient's production in return.[11] It seems reasonable to conclude that contingency does exist (cf., Hawkes & Bliege Bird 2002), and at levels that are inconsistent with TS, but without the appropriate theory, it is not yet possible to determine whether these contingency levels support RA or are instead suggestive of something else.

Several ethnographers have also provided anecdotal support for contingency. Among the Pintupi, "large game is distributed inter-domestically to members of the residential group who have shared with the hunter in the past" (Myers 1988). One Maimande informant told Aspelin that "if one doesn't give, one doesn't get in return . . . some people are specifically excluded from most distributions because they never or only rarely give any of their products to us" (Aspelin 1979, p. 317). Similarly, "the return may be made at a later date but it will be expected" among Agta sharing with those outside the household cluster (Peterson 1978, p. 40). There are also hints of contingency among several of the more assertively egalitarian groups. The "giving of food does involve an obligation on the part of the recipient to return food to the donor at some future date" among the Siriono (Holmberg 1969, p. 45) and "something must be given in return for what is received" among the G/wi (Silberbauer 1981, p. 463).

Conversely, the ethnographic literature also contains references to contingency that are consistent with generalized reciprocity, but may not be consistent with RA. The Batek, for example, explain that giving and receiving "balance out over the long run" (i.e., lifespan) (Endicott 1988, p. 118), whereas giving and receiving among the Kaingang is "not a matter of checks and balances . . . their understanding of reciprocity is in terms of lifelong symbiosis, not in terms of balanced exchanges" (Henry 1941, p. 101). Whether the benefits that accrue after the very long delays associated with generalized reciprocity outweigh the opportunity costs of giving in the present, is an important question worthy of future research.

General contingency, or the correlation between the total amount given away to others and the total amount received from all others, has been measured in six societies: Ache (Gurven et al. 2002), Hiwi (unpublished analysis), Meriam (Bliege-Bird & Bird 1997), Pilaga (my analysis of Henry 1951), Yanomamo (Hames 2000), and Hadza (Hawkes et al. 2001). These studies showed mixed support for general balance.[12] Although a lack of specific contingency contradicts RA, the presence of general contingency is consistent with indirect reciprocity (Alexander 1987; Boyd & Richerson 1989), whereby individuals other than direct recipients may confer benefits on a donor, and also with a form of CS whereby the return benefit to the donor is food. If the return benefit is in another currency, such as increased mating opportunities, then a lack of general balance is not inconsistent with CS.

Ethnographies often highlight anecdotes suggestive of trade rather than indirect reciprocity. For example, Pintupi women give food production to "those who looked after the children while she was away" (Myers 1988). The best Yuqui and Tsimane hunters appear to work less in garden labor, trading portions of their kills for garden products (Chichón 1992; Stearman 1989). Manioc is given to Kuikuyu who do not have manioc fields, in exchange for helping with weeding tasks (Carneiro 1983). Holmberg (1969) explains that Siriono men give food to their wives in exchange for sex, and that more food is given to younger wives, with whom the husbands desire to have more sex. Yanomamo men also give meat in expectation of receiving sex (Ritchie 1996, pp. 190–93).

4.4. Are slackers punished?

Another aspect of contingency is that those who do not share, who do not share enough, or who do not produce food should somehow be "punished" for their lack of cooperation, either through gossip, withholding of shares, or other group-related benefits (e.g., not invited on group hunts), social ostracism, village fission, or even violence in some cases. Although punishment has not been systematically studied in any group, there are abundant illustrative anecdotes of punishment from the ethnographic literature. For example, one Pilaga family temporarily left the village in response to giving twice as frequently as it was receiving food from another family, consistent with their common complaint, "I have given something to him but he has not given to me" (Henry 1951, p. 199). Although Mamainde food distributions appear egalitarian (quantities given to each family is inversely proportional to number of families present), Aspelin (1979) notes several cases where one unproductive family with a precarious position in the village was frequently excluded from receiving shares. Altman (1987, p. 147) describes a collusion between two Gunwinggu family clusters to share less food with a third cluster who was "not producing enough." This sanction induced higher production and sharing by the third cluster, wherein the other two family clusters resumed normal relations. Among the Washo, a "person who would not share with others of the same household, or who was generally stingy would not be included in the networks of sharing and would be 'talked out' of his household" (Price 1975, p. 16). Baksh and Johnson (1990) relate a similar anecdote in which a household that "did not like to work cooperatively, or participate in communal undertakings" was driven out of the village. An unproductive family "quickly gets pressure to contribute its own share" among the Agta, where social ostracism ultimately forces them to relocate (Griffin 1982, p. 20). Bridges (1948, pp. 374–75) describes an incident among the Ona in which a hunter who didn't share a small bird was ridiculed and humiliated with mocking bird calls by other men for *years.* Among the Netsilik Eskimo studied by Balikci (1970, p. 177), "lazy hunters were barely tolerated by the community. They were the objects of back biting and ostracism . . . until the opportunity came for an open quarrel. Stingy men who shared in a niggardly manner were treated similarly." A similar anecdote is described among the Canadian Utku, where a stingy family was relocated at some distance from the core community (Briggs 1970, pp. 219–23). Finally, Bertoni (1941, p. 39) describes how a greedy Ache hunter, getting fat from killing game and not sharing it with his thin wife, angered so many people in camp that a group of men killed him "by spearing him and then clubbing him to death."

Several anecdotes, however, demonstrate tolerance for either low producing individuals or for violations of implicit social contracts. Several Chácobo households who consistently under-produced for several years because of "poor planning, indifference, or laziness" received more than they gave away, and "were tolerated . . . they were never expelled or ostracized from the community" (Prost 1983, p. 52). Instances of pinenut stealing were never confronted because of a "desire to keep peace" among the Kaingang, although Henry also contends that "many of the conflicts within the extended families arise out of some failure to live up to the ideal of constant helpfulness and support" (1941, p. 101). Among the Siriono, older individuals sometimes steal food late at night (although they deny it), and are never punished for their actions, although they are often the subject of condescending gossip (Holmberg 1969). Endicott (1988, p. 119) describes several able-bodied adults who "seemed to take more out of the sharing network than they put in." After asking several informants why they did not try to expel one of these lazy individuals, they responded "because he is a Batek." It is interesting to note that the spouses of two of the three slackers boosted their own work effort in an attempt to compensate for the laziness of their husbands. Even when shirkers sometimes receive shares, as during net fishing events among the Maori, where "nobody went away empty," we find that "at the same time, a distinction was made in favour of the workers" (Firth 1929, p. 277). These anecdotes are consistent with conclusions from various mathematical models, which show a stable mix of cooperative and uncooperative strategies within populations (Blurton Jones 1987; Vickery et al. 1991).[13]

Anecdotes of punishment reveal the difficulties in assigning labels of "cheater" or "defector" to certain individuals, and thereby subsequently measuring contingency. Because the quantity of food *A* gives *B* is equal to the product of *A*'s production and the proportion of *A*'s production given to *B,* a failure to reciprocate can be a result of either low production or an unwillingness to share. With little producer control, a failure to share is equivalent to a failure to produce. As mentioned previously, low production can result from controllable factors such as low time investment resulting from laziness or other time-consuming responsibilities and from uncontrollable factors, including bad luck, sickness or injury, and low ability. We might expect less tolerance for low production resulting from controllable fac-

tors, although it may not always be easy to distinguish the cause of poor production. However, in small groups with little privacy and much gossip, long-term deceptions are unlikely. Although we might a priori predict that only quantities exchanged matter, several bargaining experiments reveal that intentions also matter in determining fair outcomes (Blount 1995). The fact that pregnant Ache and Hadza women reduce their work effort (Hurtado et al. 1985), and are instead subsidized by other Ache and Hadza, whereas reduced work effort might not normally be tolerated (as suggested by its rarity and by informant reports), lends support to the notion that causation can influence decisions based on fairness. Indeed, Gurven et al. (2002) argue that the sharing of non-meat items and cultigens shows high contingency, when measured in terms of quantities of food exchanged across pairs of families, whereas the sharing of meat items may show low or no quantity-based contingency (see sect. 8.2). Success rates and quantities of foraged foods (e.g., fruits and roots) produced are heavily dependent on the amount of time spent in their acquisition, whereas luck and random factors have a much greater influence on the success rates and quantities of meat items produced. "Defectors" may therefore be punished for not contributing enough labor or work effort to production tasks, rather than for not producing a certain amount of food (see sect. 8.2).

The existence of enforced norms (Axelrod 1986; Boyd & Richerson 1989; Gintis 2000; Kaplan & Gurven, in press) to share and to produce eliminates the collective action or public goods problem of group food production decisions by transforming the payoff structure from that of a Prisoner's Dilemma into that of a mutualism, whereby temptations to defect and second-order collective action problems (i.e., who should punish?) disappear. Thus, producing food (sharing some, and receiving some when others produce food) has greater payoffs than relying on your own solitary food production. Hunting with sharing is a viable provisioning strategy, especially given the rich proteins and lipids found in animal products and the complementary carbohydrate-focused subsistence decisions of women, even though mens' focus on game production may be motivated, in part, by the mating benefits that accrue from CS (Bird 1999).

5. What is the value of reputation?

When asked why they often feel compelled to give away shares of production to others, many informants often report either a group-oriented reinforcement-type response such as 'that is our custom," or a sanction-avoidance response such as "If I don't give, others will be angry, or say I am stingy." These responses highlight the information-value of sharing, whereby giving may be a useful means of advertising a reputation for wealth or ability, generosity, or merely a lack of stinginess.[14] If producers lack control over distribution of certain resources, then their desire to pursue those resources (especially when net benefits are less than those from alternative foraging strategies) may reflect a costly signal. However, even with strong producer control, decisions to give widely may be guided by a desire to signal some attribute. Signals are easily interpretable by a large audience when they are repetitive, stereotyped, and conspicuous (Johnstone 1997; Krebs & Dawkins 1984). Giving significant portions of packages away to many other individuals is a ripe opportunity to gain abundant status points. Game animals are usually the most culturally valued, perhaps because of the difficulty in acquiring them and their high nutrient density; these items are typically the most widely shared of all food resources. Among the Maori, when hunters brought in large quantities of fish, birds, or rats, women would "dance, caper about, and chant an *umere* or song of joy" (Firth 1929, p. 276). Good hunters are usually accorded much prestige. Good hunting ability is accorded high status among the Siriono (Holmberg 1969), Ache (Clastres 1972), Gunwinggu (Altman 1987), Yuqui (Stearman 1989), Dobe !Kung (Lee 1972), Nyae Nyae !Kung (Marshall 1976), Copper Eskimo (Damas 1972), Agta (Griffin 1982), G/wi (Silberbauer 1981), Pilaga (Henry 1951), Andamanese (Radcliffe-Brown 1922), and presumably others not mentioned here (cf. Wiessner 1996).

Although Dowling recognized over thirty years ago that imbalances in production and distribution are often corrected through "a counterflow of esteem and influence to the person who contributes the most" (Dowling 1968, p. 505), no study has ever measured whether the tangible benefits that arise from such esteem outweigh the costs of giving. The fact that the highest producers among the Ache, Pilaga, Hiwi, and Yuqui consistently gave away more than they received, compared to their poor producing counterparts (Gurven et al. 2000a; 2000b; Henry 1941; Stearman 1989), suggests that the pursuit of esteem is worthwhile (especially because producer control is evident in these groups), but that we still have little understanding of the appropriate return-benefit currencies. Successful Meriam hunters have higher age-specific reproductive success, higher quality mates, and more sexual partners than poor hunters (Smith et al. 2003). Ache women are more likely to report good hunters as extramarital lovers than poor hunters (Hill & Kaplan 1988), and children of good hunters exhibit higher survivorship than those of poor hunters (Hill & Hurtado 1996).[15] Additionally, Ache who give relatively high proportions of their production away to others are more likely to receive food assistance during periods of sickness and injury which inhibit production activities (Gurven et al. 2000a). That high producers or generous individuals receive return benefits because of the prestige of giving, runs counter to the idea that leveling mechanisms (see previous discussion) exist to prevent the accumulation of benefits. However, additional mating benefits, assistance to spouses (increasing spouse fertility), increases in offspring survivorship, and social insurance are substantial benefits that need not disrupt a loosely egalitarian social structure.

CS theory may shed insight into numerous observations of apparently "useless" sharing. Hiwi women often give roots to women who already have their own roots, so that after sharing is done, none have more than they did prior to sharing (Gurven et al. 2000b). Chácobo women and men give each other manioc flour and fish, respectively, in the same manner (Prost 1983). The Batek do the same for a variety of foods (Endicott 1988), the Mbuti do the same with honey (Ichikawa 1981, p. 65), and the Agta do the same with betel nut chews (Griffin 1982). The Western Desert Aborigines have "evolved a system that compels people to share food, even when such sharing might not be strictly necessary, in order to assure that when an emergency arises . . . the relationships that require sharing between kin are strong" (Gould 1981, p. 435). These anecdotes support the

notion that the act of sharing has communication value, perhaps independent of the items being shared (Bird-David 1990; Minnegal 1997). These acts of sharing may signal intent to engage in reciprocal cooperative endeavors, rather than phenotypic quality of the acquirer. However, redundant sharing, as described here, may be a result of the small cost of giving when food is locally abundant but not easily storable. This kind of giving may act as a "raising-the-stakes" strategy (Roberts & Sherratt 1998), useful for building trust and identifying generous, dependable individuals for engaging in future cooperative relationships (see also Connor 1995).[16]

6. What about women's sharing?

The few quantitative studies that examine both male and female production and distribution patterns suggest that women do not collect food only for the purpose of household provisioning. Ache and Hiwi women share all foraged plant foods extensively, giving away about 55% of all collected food in both cases. Among the Hiwi and Ache (on forest treks and at the reservation), there are no sex differences in sharing behavior after controlling for the package size of the resources they acquire. A similar pattern is described among the Agta, who share wild plants and cultigens in the same manner as meat, and the women intentionally harvest an abundance of roots for the purpose of sharing (Griffin 1982). Both men's and women's sharing increases with larger package sizes, suggesting that men's sharing patterns are not unique. Most importantly, Ache, Hiwi, and Agta women generally return to camp carrying packages of palm fiber or roots larger than their family members can consume, and widely share these packages with individuals outside their nuclear family. Any gathered food or cultigen comes in small increments and so production levels are subject to an acquirer's control. Any woman could stop working whenever she had enough food for her family. These women must therefore overproduce collected foods intentionally because they gain some benefit from the food they transfer to others. Unlike the classic payoffs to males assumed in "showoff" and most CS models, the gains from sharing by women cannot be increased number of mating partners (cf. Beckerman & Valentine 2002). Instead, the gains from sharing must be in some form that affects women or their offspring.

If women's sharing benefits offspring, then men's similar sharing patterns may very likely also benefit offspring. The fact that only men choose the variance-prone foraging strategy of hunting cross-culturally, whereas women focus their subsistence efforts on predictable gathered foods, is consistent with the notion that men are more likely to be motivated by CS than are women. However, alternative explanations are likely. In general, a sexual division of labor is expected when multiple currencies (e.g., protein-lipid, carbohydrate) provide utility, when the activities that produce them are mutually exclusive, when either sex has a comparative advantage, and when high productivity requires a relatively long training period. Under these conditions, specialization is so efficient as to be inevitable (Becker 1991). The ecology of many foragers is consistent with these requirements, and thus the specialized divisions of labor so common in most foraging societies do not require CS to explain them. In fact, the applicability of CS models to daily activities, which provide the bulk of household food production, may be rather limited. CS is probably most useful for understanding instances of "conspicuous consumption," which may occur as relatively infrequent activities such as potlatches among Northwest Coast Indians, and feasts among the Maori (Boone 1998; Firth 1929; Jonaitis 1992).

7. Multiple currencies and multivariate analyses

An individual can give away shares to benefit kin, to receive like shares in the future, to avoid high defense costs, and/or to receive some other fitness-enhancing benefit either at the time of distribution or on a future occasion. Evaluating the relative impact of different payoffs on the variation in sharing behavior across individuals within a population, or even within individuals over time, will require a systematic way of comparing the expected magnitudes of benefits associated with each hypothesized motive for food transfer. A KS component would include the net boost of food on the reproductive value of kin. A RA component would include the expected time-discounted return benefits of receiving either like food resources or other fitness-enhancing items or services. A CS component would require estimates of the fitness value of having established one's "high quality" to the audience composed of witnesses to the high production (and redistribution) activities. It is important to recognize that giving a certain amount of some food resource is expected when the *sum* of these time-discounted benefits outweighs the present costs of giving. This means that the different payoffs can all contribute to the final decision to share food. If an individual shares food when the sum of these benefits is less than the immediate costs of giving, then we may conclude that TS or some other explanation accounts for the behavior.

The overlapping predictions of sharing models require sharing analyses to incorporate multiple influences simultaneously, rather than examinations of single variables on sharing outcomes. However, detailed multivariate analyses of factors associated with different levels of sharing have been published for only two groups: the Hiwi of Venezuela (Gurven et al. 2000b) and the Ache of Paraguay (Gurven et al. 2001; 2002). At the time of study, the Hiwi population contained 37 nuclear families (106 individuals) who were living at a permanent settlement, with wild foods composing 95% of the diet. The Ache reservation sample contained 25 nuclear families (121 individuals) and was also based at a permanent settlement, with farm foods providing the majority of the daily caloric intake, in addition to traditional forest foods. The Ache forest sample consisted of four two-week treks by bands that contained 10 to 14 families (17 to 48 individuals), and where wild foods composed over 95% of the daily diet. Multivariate analyses focused on two questions: (1) What affects the percentage of food production given to other families? (2) What affects how much family *A* gives to family *B* over the sample period?

Figures 2 and 3 show the results of path analyses meant to answer these two questions for the Hiwi.[17] As mentioned previously, the Hiwi results indicate that donor sex and age have no impact on giving when other relevant variables are included in the same analysis. Resource package size and a measure of resource acquisition "variance" have strong separate positive impacts on sharing depth, whereas the num-

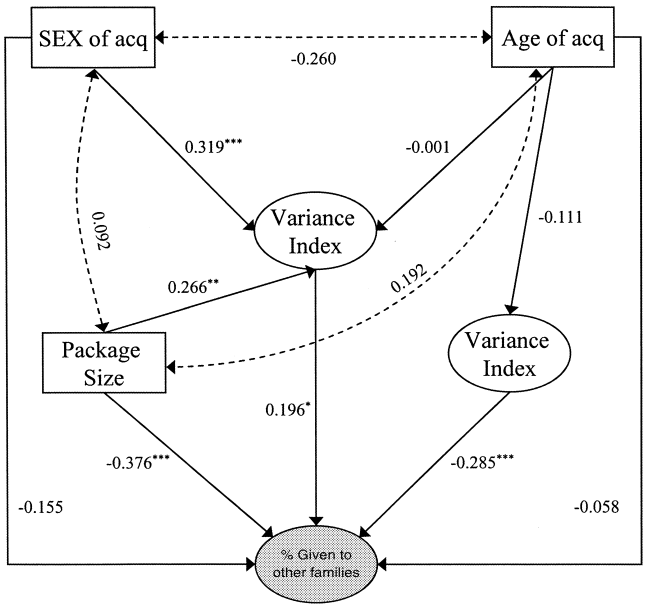

Figure 2. What determines how much a Hiwi acquirer keeps in the nuclear family? Numbers are standardized coefficient estimates from a path analysis model. Note that $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$. Variables in boxes are extrinsic variables, those in ovals are intrinsic to the model. "Variance Index" for a given resource is defined as $A(B + C)$, where A = degree of asynchronicity in acquisition among individuals, B = variation in encounter rates per person hour spent in search, and C = variation in energy obtained per pursuit. For overall model fit, $p = 0.354$ from a chi-squared test, Bentler's and Bonett's NFI = 0.981, Bentler's CFI = 0.996. Sample includes 130 sharing events.

ber of individuals in the donor family has a negative impact on the percentage of food given to other families (Fig. 2). Large, risky resources are shared with greater breadth than smaller, predictable resources, and small families give away more than large families. The size of a recipient nuclear family and the percentage that family gave to a donor family each have strong, positive independent effects on the percentage of food the donor family gave to that recipient family (Fig. 3). Thus, contingency and recipient need are significant predictors of sharing depth even when controlling for kinship and spatial proximity of households. The multivariate analysis also suggests that the positive effect of kinship on giving may be an artifact of residential distance, which acts as a stronger predictor of giving than kinship. One interpretation of this kinship and distance relationship is that close kin who desire to share with each other according to RA choose to live within close proximity to each other, as suggested by the correlation, $r = 0.5$, between kinship and proximity.

Multivariate analyses of sharing among Ache during temporary foraging treks and at the reservation settlement have found similar effects of donor family size and resource package size on the percentage given to other nuclear families (Gurven et al. 2002). Additionally, the number of individuals present on a trek was positively associated, and the total daily food production of a specific resource type was negatively associated, with the percentage of that resource type given away to other families on foraging treks, consistent with both TS and RA. In both forest and village settings, a significantly larger percentage of meat resources was given away compared to other resource types, even after controlling for the size of those resource packages. Distances between households and their relative visibilities were strong predictors of the total quantities of food exchanged among specific families in both Ache settings. Two important differences found when comparing forest and village contexts are noteworthy: kinship and contingency have little effect on receipt of meat in the forest, whereas these variables exhibit strong effects at the reservation. However, kinship and contingency are strongly correlated with increased giving of nonmeat items among pairs of families during foraging treks, suggesting that much of the variation in interhousehold sharing patterns across settlement and forest may be a result of differences in the production systems that produce different kinds of foods, rather than any magical qualities associated with meat. I explore this relationship in the next section.

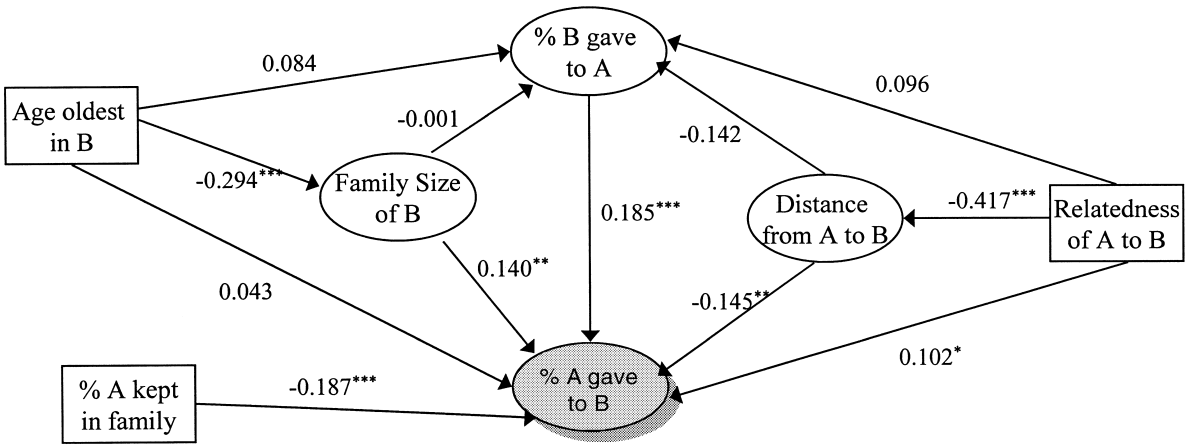

Figure 3. What affects how much Hiwi family A gives to family B? Numbers are standardized coefficient estimates from a path analysis model. Note that $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$. Variables in boxes are extrinsic variables, those in ovals are instrinsic to the model. For overall model fit, $p = 0.008$ from a chi-squared X^2 test, Bentler's and Bonett's NFI = 0.921, Bentler's CFI = 0.943. Sample includes 210 family pairs.

8. Production and distribution: Food versus work effort

Two general patterns of sharing are apparent from the review presented: high sharing depth and breadth with little to no contingency between giving and receiving, and restricted sharing depth and breadth with significant contingency. These patterns represent two extremes along a continuous range of sharing patterns, which may be loosely identified with generalized foragers on the high sharing end, and horticulturalists on the low sharing end of the spectrum. The most important ecological feature that influences the costs and benefits of giving is the suite of profitable resources available as preferred foods which are a function of extraction technology, cultural knowledge, and the social relationships that negotiate the relationship between food production and distribution. This relationship is probably responsible for much cross-cultural variation in transfer patterns. Although group size and spatial distribution of individuals, which act as proximate influences on sharing, are also important, these variables probably derive from requirements of the production system.

8.1. Resource ecology

The degree to which the diet is composed of large, asynchronously acquired foods should affect overall breadth and depth of sharing, because, under these conditions, others' level of need is high whereas costs of sharing are relatively small. The two extremes are exemplified by diets consisting primarily of difficult-to-acquire bulky meat packages, which arrive intermittently at camps, as in assertive egalitarian groups, and those consisting primarily of small, predictable, relatively easy-to-harvest carbohydrate bundles, as in forager-agriculturalist groups. Predictable, cultivated and gathered food items are shared with less depth and breadth than meat items in all societies where this has been investigated, including the Ache (Gurven et al. 2001; Kaplan & Hill 1985), Hadza (Hawkes et al. 2001), Hiwi (Gurven et al. 2000b), !Kung (Lee 1979), and Yanomamo (Hames 1990). Although meat items tend to come in larger packages than non-meat items, and resource package size correlates strongly with increased sharing depth and breadth, meat items are still shared more widely among Ache, Hiwi, and Yanomamo when controlling for differences in resource package size. Much of the variation in cultural-specific sharing depth and breadth is partly a function of the variation in diet composition among groups. It is important to note that non-meat items such as roots, berries, fruits, and grubs, are often shared with nontrivial depth and breadth, as reported among the Ache (Kaplan & Hill 1985), Yanomamo (Hames 1990), and Kubo (Minnegal 1997). Risk- or variance-reduction RA, TS, and CS, however, cannot explain why these characteristically "unrisky" food items are shared at all, yet transfer of these foods is substantial. Where fixed costs (such as travel to a resource patch) are high relative to total acquisition costs, over-production with sharing of non-meat items, in combination with an economy of scale and contingent turn-taking is a profitable option (Gurven et al. 2001; Hames 1990; Kaplan et al. 1990). Sharing of these collected and harvested foods may occur when trust and widespread sharing are already established because of reliance on more risky resources. Thus, the Ache share the same horticultural foods more intensively and with greater breadth than do the Guarani living in surrounding communities who do not share meat extensively as do the Ache.

8.2. Food production

The diets encountered among different groups should not be viewed as extrinsic characteristics of those groups. Indeed, the four evolutionary models discussed in this paper (KS, RA, TS, and CS) ignore most characteristics of the production system that generate food items found in the diet. The only aspect of production addressed by these models is the degree of acquisition variance based on luck, but these models are silent about the underlying causes leading to such variance. Production will depend on the kinds of high caloric return resources available in the local environment, the available extraction technology and knowledge required to convert "resources" into food, and the social arrangements necessary to achieve coordinated production (Alvard & Nolin 2002). If a food item produced by a solitary individual is shared differently than a jointly produced item, especially when multiple individuals are critical to the production process, then group-oriented production processes contribute an additional motivation for food transfers. Decisions about producing food and subsequent distribution are interdependent, such that focusing on one without the other misses an important component of social and economic behavior (Firth 1929; Hawkes 1993; Hill 2002; Hill & Kaplan 1993; Minnegal 1997; Winterhalder 1996b). If substantial portions of certain resources are routinely given to others and little is given back in return, then the expected net caloric return rate for personal consumption may be low, so that widely distributed foods should drop out of the optimal diet. Similarly, items that reduce the long-term average caloric return rate may be pursued zif the use value of those items (through trade, group production, signaling information, body adornment, etc.) inflates their worth. For example, Fanalei hunters in the Solomon Islands eagerly accumulate dolphin teeth to use as bride wealth payment, adornment, and monetary currency (Takekawa 1996). Thus, notions of producer control, and sharing breadth and depth, may be best thought of as negotiated norms, rather than as extrinsic influences on production decisions.

Prosocial foraging behavior, by definition, requires that individuals associate in groups. The degree to which groups of individuals share together may be related to the degree to which they forage together. The extent to which production relates to distribution should reflect the degree of coordination and/or specialization in the production process. Indeed, group production varies in the extent to which it should be labeled cooperative. Three possibilities for group production include: (a) simultaneous solitary foraging, whereby the presence of other individuals has little effect on personal production, (b) mutualism, whereby group cooperation is compatible with each cooperator's individual interests (i.e., no temptation to defect), and (c) prisoner's dilemma or public goods-based cooperation, whereby group interests conflict with benefits that can accrue to defecting individuals. Simultaneous solitary foraging seems to describe group hunts by Gombe chimpanzees (Boesch & Boesch-Achermann 2000), whereas mutualism seems to describe group hunts by Tai chimpanzees (ibid.), social carnivores such as African wild dogs and Serengeti lions

(Dugatkin 1997), fishing among the Ifaluk (Sosis 2001), whaling among the Lamalera (Alvard & Nolin 2002), and net hunting among the Aka (Kitanishi 1996).

To the extent that all individuals on group hunts increase their daily per capita intake through a combination of an increased prey encounter rate, decreased search costs, or an increased probability of pursuit success, relative to that from solitary hunting, human hunting may be labeled as mutualistic. In fact, many types of cooperative hunts are not possible without some minimal number of participants, and so success occurs at a group level (e.g., net hunting, whaling, game drives). For group hunts, and solitary hunts where band members pool the catch at the end of the day, all members may still gain mutualistic benefits. However, it is more likely that some individuals fare better than others by either engaging in any particular group hunt, or in the decision to pool kills at the end of any particular day of solitary hunting. Over a time span of days, months, or even years, however, those same individuals who could have fared better after a single event, are likely to gain net benefits if they receive food during times when they acquire little to none. Thus, it has been argued that the ability to reap gains from cooperation via reciprocity, as opposed to mutualism, depends on species-typical rates of discounting the future (Clements & Stephens 1995).

Despite the potential gains of cooperative foraging, the few long-term data on individual hunting return rates among Ache and Efe men indicate consistent differences in hunting success and caloric efficiency over time (Bailey 1991; Hill et al. 1987). If these men consistently give more than they receive, then the possibility that high producing individuals gain net insurance benefits from sharing, or any other status-derived benefit is an empirical question that requires a better understanding of how different feeding regimes affect long-term survival and fertility (Gurven et al. 2000a). It may, however, be the case that the costs of sharing are not paid back on average to high producers. In modern societies, many individuals pay years of auto, life, health, and homeowner's insurance premiums and never make any substantial claims that outweigh the summed premium costs. In general, these are wealthier individuals who can more easily afford the luxury of insurance coverage and who want to avoid the risk of catastrophe. This is consistent with the observation that the highest producers in foraging societies are the ones most likely to give away more than they receive (see sect. 4.3). Norms of giving enforced by sanctions as a means of punishing stinginess can "force" high producers to pay graduated income taxes. In this respect, giving may be regarded as a form of TS where the cost of not giving is a verbal or cultural sanction, especially when the number of high producers is small relative to the number of average to low producers. However, norms of sharing that benefit older individuals (at the expense of young high producers) will benefit those young individuals later in life when their dependency is relatively high. This is the same social convention that has led to social security programs in modern state societies, and so perhaps it is not surprising that it emerges amongst foragers as well.

Although contingent sharing of specific quantities of food may not exist in several egalitarian societies, "contingency" of a different form may be more appropriate in groups where individuals coordinate various subsistence-related tasks for mutual benefit. Where random, uncontrollable factors contribute a significant portion of the within-individual variation in production returns, maximum group production requires a sufficient number of person-hours to be invested in food obtaining activities. If food is pooled equally among group members, then maximizing per capita production is equivalent to maximizing group production. A contingency system may evolve which therefore rewards work effort rather than actual returns. Sufficient work effort requires the kinds of sanctions against laziness previously mentioned, even if producer control is lacking and sharing is an automatic outcome of resource characteristics and recipient demand. In commenting on the work contributions expected from visiting Aka, Bahuchet (1990, p. 41) reports that "if one stays longer [in the group] it is also necessary for him to participate in production activities." The roots of equity and fairness considerations in such economies may be based on effort and time investment rather than on strict outcomes. When random factors significantly affect production, effort and output may not be strongly correlated. Controlling for individual ability, the number of hours per day Ache men spent hunting while engaging on foraging treks had no effect on daily returns, and there was no quantity-based contingency for game sharing. However, in economies with more predictable diets, effort and output are more highly correlated, and contingency based on output is more likely (especially when effort is more difficult to monitor). Thus, among the Hiwi, men's work, effort was highly correlated with daily hunting returns, and the contingency of meat sharing, as measured in quantities exchanged, was strong.

This view suggests that time, labor contributions, and intent are important indications of commitment, and may reflect the social contract that defines the redistribution characteristic of many small communities. As discussed earlier, there are many ethnographic examples of hunters pooling catches among themselves in a first wave of sharing, consistent with the notion that "work transforms material things into property" (Barnard & Woodburn 1988). The Mbuti (Bahuchet 1990), Aka (Kitanishi 1998), Washo (Price 1975), Hiwi (Gurven et al. 2000b), Pintupi (Myers 1988), Northwest California Indians (Gould 1981), Netsilik Eskimo (Damas 1972), Lamalera (Alvard 2002; Alvard & Nolin 2002), Nyae Nyae !Kung (Marshall 1976), Inujjuamiut (Smith 1991), Makah (Singleton 1998), Fanalei (Takekawa 1996), and Maori (Firth 1929) each have sharing norms that encourage initial distributions to other hunters who participated in the hunt. For example, cooperative hunts of hare wallabies and hill kangaroos among Pintupi Aborigines traditionally resulted in portions distributed to "all who participated in the hunt" (Myers 1988). The Hiwi always share capybara among all members of the one or more canoes that coordinate their movements in the pursuit of this aquatic game species (Hill, personal communication). When Ache or Tsimane hunters go on day hunts from the village in pairs, they almost always share killed game with their hunting partner. Bailey (1991) reports that following group hunts among the Efe Pygmies, initial game distributions are biased toward participating members in the hunt, and that portions are allocated according to the specific hunting task. Thus, the hunter who shoots the first arrow gets an average 36% (and the most highly prized liver), the owner of the dog who chased the prey gets 21%, and the hunter who shoots the second arrow gets only 9% by weight. Although mutualistic payoffs might encourage participation in group hunts, these payoffs are only insured through rules of distribution that benefit participants.

When the hunting task group includes all men present in camp, task group sharing and residential group sharing may be indistinguishable. When residential groups are not much larger than the hunting task group, preferential sharing in the first wave may be evident, but subsequent sharing may result in all band members consuming similar meat portions. Additionally, if prestige accrues from distributing shares, then recipients of shares from initial distributions who later redistribute portions to other have-nots gain additional status. With large residential groups, task group-based sharing can lead to exclusions of a significant number of band members.[18] Group size in many circumstances may be a reflection of sharing networks, rather than a proximate determinant of transfers (Smith 1991). Even foragers that live in small groups, however, occasionally congregate in larger groups for feasts, ceremonies, or fights, whereby opportunities for more extensive food transfers, and hence costly signaling, exist. In larger village communities, it is not uncommon to find – as among the Ache and Tsimane – widespread food transfers on special occasions, such as childrens' birthdays, village-wide feasts, and during visits by neighboring peoples.

8.3. Bandwide sharing

The exceptions to production task group sharing are extreme band-wide distributions that occur whether or not other recipients were members of the hunting group, or even whether or not they hunted at all. This form of sharing may be relatively rare cross-culturally, and generally occurs only in small bands of less than 40–50 individuals. This often occurs in the distribution of very large game (relative to the band size), as among the Gunwinggu (Altman 1987), Hadza (Hawkes et al. 2001), !Kung (Lee 1979), Ache (Kaplan & Hill 1985), Kubo (Dwyer & Minnegal 1992), Inujjuamiut (Smith 1991), Western Shoshone (Steward 1938), Owens Valley Paiute (Steward 1938), and Fanalei (Takekawa 1996). However, wide distributions of even small game items have been described for the Hadza and Batek. Among the Ache, large cooperatively acquired game were shared no differently than game acquired by solitary hunters (Kaplan & Hill 1985). As described earlier, some foraging bands maintain norms of widespread meat sharing, contingent on the contribution of some meaningful productive work that may benefit others. In these cases, the cooperative unit or "resource-sharing group" (Minnegal 1997) is not the hunting task group, but the entire (or a subset of the) band. Even if sharing is because of TS, if individuals who do not produce (and who are therefore not eligible to share) are ostracized or receive some form of punishment, then the resulting "reciprocal" TS, where individuals take turns playing the role of acquirer and recipient but then share according to TS post-acquisition, is essentially identical to RA.

In these cases, we should instead find receipt of shares contingent upon time and effort spent in food production, or production-related work. A division of labor by sex, age, and skill enables individuals to specialize in activities for which they substitute at the highest return rate (Gurven & Kaplan n.d.). This division of labor rests on the assumption that members within a cooperative unit (be it a nuclear family, a subset of the group, or the entire band) have access to the pooled food production. On extended foraging treks, 17% and 11%, respectively, of Ache men's and women's foraging time were spent engaging in activities that were intended to increase others' caloric production rates at the expense of their own (Hill 2002). For example, some individuals cut trails, carry game and other items for others, indicate resource locations for others to exploit, flush monkeys so others have a clear shot at them, call others to fresh spoor, and leave some resources such as honey and armadillos for others to pursue while they continue searching. This high degree of cooperation may explain why game is given to those who did not hunt, and why gathered and collected items are often shared outside the nuclear family (especially when harvesting involves economies of scale as mentioned in sect. 8.2). Similarly, among the Lamalera, those who never participate on whale hunts, but who contribute labor as specialist sail or boat makers, receive substantial portions of whale meat (Alvard, personal communication). Dwyer and Minnegal (1993) show that most Kubo men hunt, but differ significantly in their hunting returns because they specialize in both their hunting tactics and the animals they pursue, and that sharing is both widespread and unconditional.

8.4. Restricted sharing

Many groups, however, do not engage in bandwide sharing of meat items, and instead restrict initial sharing to the task group or extended family, with only subsequent sharing with other group members, although as mentioned earlier, primary sharing can be extensive when very large quantities are produced. In many groups this pattern is viewed as "fair." Future research should focus on understanding the conditions that favor different norms of sharing and perceived fairness. Interdependent subsistence, small group size, high average relatedness to group members, coordination in residential structure, and outside threats, may all favor increased within-group sharing. Increases in group size, weak punishment against slackers, and shifts in diet towards smaller, more predictably acquired foods may instead promote more self-sufficiency (e.g., storage) at smaller levels of social organization (i.e., the nuclear family). Thus, among Northwest Coast Indians, Gould (1981, p. 451) reports that "each family was able to collect, prepare, and store its own food resources largely by its own efforts," and that "all food was redistributed with the clear expectation of immediate repayment, either in labor or in prestige goods." Moulton and Dunlay (1983, p. 259) provide similar evidence with the Nez Perce of the Columbian River plateau.

9. Conclusion

Available cross-cultural evidence of production and distribution patterns among small-scale societies cannot rule out RA as a primary model of food transfer, whereas the relevance of TS in recent treatments seems overstated. The idealized conditions required for widespread TS may be rare cross-culturally. This suggests that the delayed benefits from hunting need to be included when considering whether hunting is a viable subsistence strategy. Few explorations of these returns have been done systematically. Although most investigations examine simple tit-for-tat reciprocity, more complicated social arrangements, including those whereby important social support is pro-

vided only if one adheres to socially negotiated sharing norms, seem more appropriate. Although men's focus on game production may be motivated, in part, by the mating benefits of signaling, hunting seems to be a viable provisioning strategy, given the subsistence decisions of women, and does not require costly signaling to justify its widespread occurrence.[19]

Despite the compulsory nature of giving in many small-scale societies, patterns of giving and receiving are sensitive to costs and benefits affected by the types and sizes of foods being shared, others' labor contributions to resource production, and other bargaining arrangements. The weighting of fitness benefits and costs yields the conditions of giving from an "ultimate" gene's eye-view. However, individuals may give for reasons that seem contradictory with one or all of the genetic subcomponents, if based on proximate psychological and emotional motivations invoked under different or novel circumstances, or if based on adherence to group-level norms or heuristics that differentially benefit certain individuals. Some of the difficulties in understanding sharing behavior stem from a confounding of the levels of analysis: proximate motivations, cultural prosocial norms that partially correlate with actual behavior, and outcomes in terms of genetic fitness. Although all behavior influenced by natural selection must, by definition, be explicable in terms of differential genetic replication in an ancestrally relevant environment, the link from individual behavior to genetic selfishness need not be straightforward. Altruistic, prosocial, and self-interested behavior at the individual level may all be consistent with genetic selfishness. Revisionist theories in psychology (Caporael et al. 1989) and economics (Bolton 1991; Rabin 1993) have recently been developed to incorporate principles of equity, fairness, or others' utility into personal utility functions, in an attempt to explain why human subjects in various experiments act prosocial when the extrinsic conditions of these experiments predict widespread defection. These models may help us understand how individuals make cooperative decisions at a proximate level, but the reason why any specific utility function supports empirical findings will require an ultimate-level explanation that links evolved psychology or heuristics to fitness in a specific environment. For example, although signaling generosity is costly in the short-term, long-term benefits may accrue in societies where there are frequent opportunities for cooperative gain, when payoffs to cooperation at these opportunities are substantial, and when the choice of cooperative partners is based on observations of past generosity. Preliminary results of economic games designed to measure propensities for generosity in many traditional societies support this view (Henrich et al. 2001b).

Rather than assuming any universal tendencies for humans to cooperate extensively in all ancestral-like contexts, human behavioral ecology has been successful in sparking systematic inquiry into the whys and wherefores of costly giving. By linking the transaction of giving with long-term insurance benefits, reputational investments, and mating interests of male and female actors, behavioral ecology has generated abundant useful predictions which when tested in many societies should greatly increase our understanding of human social behavior. Tastes for fairness are hardly "innate," but are also not considerably flexible; widespread equality that is mutually beneficial is only maintained with careful monitoring and enforced norms in a limited number of foraging societies. Humans may indeed include others' welfare in their personal utility functions (Bolton 1991; Rabin 1993), and such utility may be proximately guided by emotional responses (Frank 1988), but these predispositions can result in widespread fermented manioc, or chicha, drinking among almost all members of a Machiguenga, Huaorani, Piro, Shuar, or Tsimane village, at the same time that smoked peccary meat may be consumed only by household members while in the presence of hungry others. Although unsolicited giving varies substantially, direct appeals for food, when not excessive, are rarely denied cross-culturally, although the levels of direct requests do vary. Economics and psychology can benefit by a greater focus on the ecological conditions that favor or disfavor voluntary and involuntary giving, as highlighted by the evolutionary-based explanations described in this article. Experimentalists should also be concerned about how game stakes, or "windfalls," are presented to participants, and how interactions with other participants, in relation to the production of the "windfall," can influence giving and punishing behavior (see Kameda et al. 2002). A deeper understanding of individual tastes for fairness and giving may also help provide additional insight into the ways that people's beliefs about the poor, and the way they attribute causes for the poor's misfortune, can influence strongly held views about social welfare reform (Fong 2001).

There are still many gaps in our understanding of why individuals give differently within and among groups. In particular, future work should help bridge cognitive and psychological motivations, actual outcomes, long-term consequences of behavioral dispositions and behaviors on fertility and survivorship, short-term and long-term costs of withholding food, aspects of sharing that constitute strong signals, and the mechanics of multiperson negotiations in effecting appropriate enforceable social sharing norms. More long-term research is also needed to bridge our understanding of short-term reciprocal altruism and the kinds of long-term reciprocity that tend to reflect cultural emphases on lifelong balances. Finally, more multivariate quantitative analyses, combined with detailed ethnographic descriptions of social norms, violations, and perceptions of fairness and equity, will reveal much insight into human cooperation.

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NOTES

1. Hames (2000) independently defines depth as "sharing intensity," although from the perspective of a recipient rather than that of a donor. Breadth is defined as "sharing scope."

2. I use the terms "transfer" and "sharing" interchangeably even though sharing implies intentionality and active giving, whereas transfer is a more neutral description. Ethnographies rarely distinguish between the two usages.

3. This important condition has rarely been tested empirically

because estimation of B and C requires knowledge of hunger levels, the utility of macronutrients contained within the food, and any current resource holdings of the donor and potential recipients that are liable to influence the marginal value of receiving shares (Winterhalder 1996a).

4. Within kinship categories of equal *r*, we should also expect individuals whose reproductive value will increase the most from consuming shares to receive more, than those for whom food has a smaller impact (flow of food from old to young, haves to have-nots) (Rogers 1993), because the former yields a greater inclusive fitness benefit to the donor.

5. To the extent that individuals give food to a sick producer, in the expectation of receiving future shares from the producer upon recovery, the donor's initial giving may be thought of as a form of RA, whereas others helping the sick producer recover may be viewed as a form of byproduct mutualism.

6. Although computer simulations reveal that significant correlations between individuals in amounts given and received are possible when tolerated theft is the sole cause of food sharing, correlations greater than 0.2 were only found in highly structured groups of few individuals.

7. It may be argued that individuals who consume all of a resource outside of camp could be punished or ostracized, and that this threat is sufficient to motivate individuals to return to camp with the majority of their catch. However, the likelihood of getting "caught" eating food acquired away from camp may be low, and punishment will not bring back the food already consumed, so few should be willing to incur the costs of punishing hoarding individuals (but see Gintis 2000).

8. Although acquirers may be willing to pay higher costs to defend small resources, if others' utility for the same food is also high, then they should be willing to pay higher costs to obtain access to portions of these small items.

9. Contrary to these views, Woodburn (1998) argues that Hadza hunters get no benefits from sharing other than the "satisfaction" of completing a "difficult task."

10. Because of the format of the data available for the Pilaga, I estimated contingency as the correlation between the percentage of family *A*'s consumption (above *A*'s own contribution) provided by family *B* and the percentage of *B*'s consumption (above *B*'s own contribution) provided by *A*.

11. In regression analyses of percent given on percent received, the correlation coefficient, *r*, is equivalent to and carries the same interpretation as the regression coefficient, β.

12. Correlations of general contingency are similar in magnitude to those of specific contingency, although they are less likely to be statistically significant, because the number of observations in general contingency analyses is equal to the number of individuals or families (n). Specific contingency analyses have a sample size of $n\ (n - 1)/2$.

13. Vickery et al. (1991) show that among groups consisting of producers, scroungers, and opportunistic foragers, all three strategies can stably coexist in the same population. Defectors or "scroungers" do not proliferate when producers maintain sufficient control over their kills, when group size is moderate, and when opportunists are not very efficient. Thus, if some scroungers are tolerated (and perhaps provide other benefits), it can still be in producers' interests to continue acquiring food.

14. If one is known as too generous, others may attempt to exploit them. Thus, people are more likely to give donations when confronted with direct requests, than to give on their own initiative. The desire to avoid requests for money may be an important explanation for anonymous giving to charities (Cicerchi & Weskerna 1991).

15. With a small sample, Dwyer and Minnegal (1993) showed that skilled Kubo hunters did not show higher reproductive success, when measured as the number of legitimate births, than poor hunters.

16. I thank Kim Hill for the analogy of people purchasing small items on credit to build up their credit record so that they can later secure larger credit limits, or bank loans to purchase more expensive items.

17. Path analysis is a useful tool for examining the separate effects of multiple, often codependent, variables related through some causal process (Loehlin 1987). Path values are usually expressed as standardized parameter estimates, where one standard deviation unit increase in the variable at the base of each arrow causes an increase in the variable at the head of each arrow equal to the parameter estimate, also given in standard deviation units. These path values control for all other effects in the model, and allow one to calculate both direct and indirect effects of predictor variables on the outcome variable of interest.

18. When residential bands increase in size because of nonforaging related benefits of grouping (e.g., mating opportunities, proximity to missions or nearby towns, defense against hostile neighbors, etc.), traditional group fissions like those described among the Yanomamo, Ache, Tsimane, and the Penan (Brosius 1990) are more unlikely, and thus, more restricted sharing networks and more stringent contingency can result. As Prost (1983, p. 63) discusses, among the Chácobo, access to market goods has caused larger villages (12–15 nuclear families instead of 6), an absence of traditional fissioning, and a lack of widespread sharing with everyone in the group. He argues that once group size moves beyond 35–45 people, sharing shifts from an intimate "uncalculated" pattern to one based on "rational, reciprocal, cost-benefit calculations." The fact that individuals have the ability to make this shift and perform well in both small and large group contexts suggests that highly variable group size may have been common in our evolutionary past.

19. Even if TS explains some meat distributions, enforced norms of widespread meat sharing followed by a group of hunters can yield reliable shares of meat over time. Thus, even TS-based sharing can make hunting a viable provisioning strategy.

Open Peer Commentary

Good hunters keep smaller shares of larger pies

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Abstract: High producers are motivated to hunt in spite of high levels of sharing because the transfers come from absolutely larger amounts of resource. In the context of a generalized cooperative subsistence strategy, stinginess could provoke the withdrawal of cooperative partners and result in a loss of income. Good producers could have more to lose by not sharing than poor producers would.

I want to focus my comments on some confusion that revolves around the observation that good and productive hunters give away increasing proportions of their harvest. At one point, Gurven compares this well-documented pattern to a graduated income tax (target article, sect. 8.2, para. 4). What seems to be overlooked is that while high producers contribute more effort, they also produce more goods. To follow the tax metaphor, although a 35% tax bracket takes a larger proportion of wealthy people's income compared to the 10% paid by low-income folk, it does not discourage folks from striving to become millionaires. Just as high-income folks in our society benefit from their productivity

in spite of their transfers via tax payments to the common good, hardworking and skilled hunters benefit from their activities while at the time transferring significant quantities of meat to others. Good hunters *can* provide more food for their family *and* more public goods. There is no logical incongruity here. Good, hardworking hunters may be getting relatively smaller portions, but they keep them from quantities that are absolutely larger. As long as there is a positive relationship between individual income and work effort, skilled producers will be motivated to work harder in spite of the fact that they are giving much away – up to a point.

While this explains why high producers are motivated to produce in spite of losses to sharing, it still begs the question why hunters (and wealthy taxpayers) do not benefit even more and keep all of their wealth to themselves. The answer might be that they would *not* benefit more if they try to keep a larger proportion of their earnings. This makes sense if the transfers take place within a context of a generalized cooperative subsistence strategy.

This is the context found among the Lamalera whale hunters with whom I work in Indonesia. Resource acquisition in Lamalera is a classic example of coordination among not only the hunters but also a range of specialists without whom the hunt would be impossible (Alvard & Nolin 2002; see also Barnes 1996). The high returns that cooperating individuals receive from whale hunting are unattainable by solitary hunters. This is true for even the best and most highly skilled and hardest-working of the hunters, the harpooners.

Gurven does not seem convinced that good producers get paid back for their efforts (sect. 8.2). Individuals have a network of personal relationships defined by age, sex, and kinship. The networks are maintained across a variety of contexts focused around mating, parenting, subsistence, and group defense. At Lamalera, hunters maintain control over the primary shares that they bring to their households. Secondary sharing that happens after meat is brought to the household is significant. If they were to refuse to share their meat with others outside the nuclear family, one could imagine that a hunter's network of partners might withdraw cooperation and his productivity would decline to the point where his family is actually consuming *less* food.

Meat acquisition and meat transfers can be used by hunters in a variety of ways. One possibility is that productive hunters share their bounty widely because they could not be as productive without the network of personal relationships that widespread sharing maintains. The costs of not sharing would be prohibitive to a harpooner in Lamalera. Not only would he be less attractive as a partner in the political and reproductive arena, but his ability to provide resources to his family would surely be compromised (Alvard 2003; Alvard & Nolin 2002).

Gurven (sect. 8.2, para. 4) hints at this idea when he says that "norms of giving enforced by sanctions as a means of punishing stinginess can 'force' high producers to pay graduated income taxes." If ostracism of stingy hunters includes withdrawal of cooperation in a society where cooperation is an essential aspect of subsistence, good producers have more to lose by not sharing than poor producers. This may explain how they are "forced" to pay more.

One might argue that poor producers have much to lose too if they ostracize good producers who do not share. Assuming that it is stinginess on the part of the good producers that elicits punishing, at least some of the costs are already being paid. In the Lamalera case, however, it is more complex – especially when harpooners are involved. This is because hunts cannot occur without the skills of harpooners. Ostracize your harpooner, and the boat is grounded. As I have reported elsewhere, however, there is anecdotal evidence that Lamalerans are willing to punish others for norm transgressions even at significant costs to themselves (Alvard, in press). A boat manager removed his boat's harpooner for assaulting his daughter. Not only was the harpooner punished, but so were the manager and the rest of crew, because the boat could not hunt without the harpooner.

Where's the beef? It's less about cooperation, more about conflict

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Abstract: Individuals give for two reasons. One is to get a benefit back. The other is to avoid a cost. "Cooperation" theories stress mutual benefits. "Conflict" theories stress costs. Hunters may give up part of their hunt because they get favors back, *or* because the recipients are stronger than they are and the hunting isn't as good anywhere else.

Twenty years ago, I spent 4 months in the Western Pacific on Ifaluk Atoll. Ifaluk is tiny – just 0.569 square miles in land area; and its population is small – just 446 in the summer of 1983. But some people on Ifaluk work harder than others; and other people live better.

Chiefs, in particular, work less. They spend almost twice as much time resting (Betzig 1988b; Betzig & Turke 1985) as other men of the same age. But chiefs' households take in more food, more often, from more distant kin (Betzig 1988b; Betzig & Turke 1986). Chiefs (and their successors) have more children (Betzig 1985a; Turke & Betzig 1985), and their children are better cared for. Chiefs spend more time with their children than other fathers (Betzig & Turke 1992); chiefs' wives spend more time with their children than other mothers (Betzig & Turke 1992); other people on Ifaluk spend more time with chiefs' children (Betzig et al. 1989); and chiefs (and their successors) adopt out more children than they adopt in (Betzig 1988a).

More than once, as I sat with a bad parasite in the Ifaluk lagoon, I wondered why the little people on Ifaluk put up with chiefs. And the answer was all around me. The nearest spit of land, another tiny atoll, was 30 miles to the west across the shark-infested Pacific. The nearest high island, Yap, was 300 more miles away. Dissatisfied anthropologists on Ifaluk had nowhere to go. Neither had dissatisfied subjects. Unhappy Ifalukese had two options. They could pay overbearing chiefs what they asked for, or they could set their outrigger sails to the wind and hope for the best.

Not so long before I first went to Ifaluk, in 1970, the American Museum of Natural History anthropologist Robert Carneiro published a paper in *Science* on the origin of the state (Carneiro 1970). He looked at state formations in Mesopotamia, Egypt, and Peru; and he concluded that they were all "circumscribed" zones. Poor men paid Sumerian/Babylonian/Assyrian emperors, Egypt's pharaohs, and Peru's Incas in tribute and labor *not* because emperors/pharaohs/Incas were good to them in return, but because the costs of leaving were high. The rich land between the Tigris and Euphrates, or around the Nile Delta, or in the Andes valleys was surrounded by hostile deserts and mountains. Dissatisfied subjects had two options. They could pay overlords what they asked for, or they could vote with their feet and hope for the best.

"Skew" theories take those two options into account. Studies of animal societies have looked for "social contracts" – the equal return of social benefits for social benefits. And they've looked for "social controls" – the biased return of social benefits to better fighters. Evidence of the first is relatively equivocal (e.g., Emlen et al. 1998). Evidence of the second is relatively clear (e.g., Clutton-Brock 1998). Better fighters do best where worse fighters are trapped: where the costs of running away to another good territory are high.

I think the whole of human history can be interpreted like that. The Sumerian word for "freedom," ama.ar,gi, also means "freedom to move" (e.g., Lemche 1979). Mobility makes equality; and inequality goes up where subjects can't get away. Around 5,000 years ago, in fertile river valleys bordered by mountains and deserts, subjects started to pay overlords labor and taxes. They stopped, as soon as they found a way out. In the wide open spaces of Africa and Asia, people had voted with their feet for millions of years. After 1095, they did it again in the Near East; and after

1492, they did it on the vast empty tracts of the New World. People – and the goods they needed to live – were freer to move. "In the beginning all the World was *America,"* John Locke once wrote (Locke 1690/1980, vol. 49). In the end, it would be again. What brought an end to unpopular government? I think the short answer is: two empty continents.

The models Gurven ably reviews here – kin selection (KS), reciprocal altruism (RA), tolerated scrounging (TS), and costly signaling (CS) – all return social benefits for social benefits. They leave ecological costs out. There is no doubt that foragers occasionally give away food to get the attention of mates (CS), to avoid fighting with the hungry (TS), to anticipate paybacks from friends (RA), and to keep their relatives healthy (KS). But sometimes they give social benefits away to stay on a good territory. They give up part of the hunt/catch/crop because the hunting/fishing/gathering isn't as good anywhere else. It's a little ironic, to me, that so many of the new evolutionists – the "Darwinian" psychologists and anthropologists – focus so much on cooperation and so little on competition. Where's the Darwinism? Where's the *beef*?

In *Homo sapiens* societies, as in any other animal societies, mobility is an aid to equality. Foragers are notoriously "egalitarian," speaking relatively. But no society lacks unfairness completely. Strong egalitarian ethics, like "we refuse one who boasts, for someday his pride will make him kill somebody" (Lee 1979), or "sell all you have and distribute to the poor" (Luke 18:22), or "from each according to his ability, to each according to his needs!" (Marx 1875/1980) aren't repeated where cooperation is automatic. They get said, again and again, where individuals conflict, and where the winners take more than equal shares. *Why* do they get to take more? Sometimes, because the givers have nowhere better to go.

Tolerated scrounging in nonhuman primates

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Abstract: Gurven suggests that the tolerated scrounging model has limited relevance for explaining patterns of food transfers in human populations. However, this conclusion is based on a restricted interpretation of the tolerated scrounging model proposed originally by Blurton Jones (1987). Examples of food transfers in nonhuman primates illustrate that the assumptions of Gurven's tolerated scrounging model are open to question.

Gurven provides a comprehensive review of the patterns of food sharing within groups of hunter-gatherers and forager-agriculturists, and carefully evaluates the available data with respect to functional hypotheses. He concludes that the relevance of tolerated scrounging (TS) as a model of food sharing has been overstated and that the conditions required for widespread TS to occur are likely to be rare in human populations. Here I argue that these conclusions are based on an oversimplification of the tolerated scrounging model and that the assumptions used are not in keeping with the original model of TS. This argument is illustrated using data on food sharing in nonhuman primates.

In most species of nonhuman primates, the transfer of food items between adults is a relatively rare occurrence. Where food transfers do occur, the most common situation is one in which a higher-ranking individual takes a food item from a lower-ranking individual by using aggression or the threat of aggression. As Gurven notes, Blurton Jones (1987) suggested that when an individual is unable to maintain control of a resource without paying a substantial cost to defend the food, a food possessor should cede portions to other individuals if this price of defense is greater than the additional value that could be gained from consuming the food. In the situation described above, the costs of receiving aggression from a higher-ranking individual may outweigh the benefits of consuming the food item.

Interestingly, the opposite situation has also been reported to occur, with food items being transferred from higher-ranking to lower-ranking individuals. Following a hunt, adult male chimpanzees have been observed to allow lower-ranking individuals to take portions of their meat. Acquirers sometimes beg for a portion of meat by using specific vocalisations and by holding out a hand to the meat possessor, as well as by attempting to grab for pieces. Occasionally, the possessor will appear to actively hand out portions of the meat to begging individuals.

A number of adaptive hypotheses have been proposed to explain such patterns of meat transfer, including trade for sex, grooming, and enhanced alliances. These hypotheses have yet to gain strong backing. For example, although sexual interactions have been observed to occur shortly before or after meat is transferred from a male to a female, these instances are very rare, and captive studies of chimpanzees have found that meat transfer does not correlate with increased matings (Mitani & Watts 2001) or with an increased chance of siring an offspring (Hemelrijk et al. 1999). Studies of captive and free-ranging male chimpanzees have found significant correlations between the number of times that meat is transferred within a dyad and the number of times that these males engage in coalitionary support and grooming (de Waal 1989; 1997b; Mitani & Watts 2001; Nishida et al. 1992).

Although these data are consistent with the suggestion that meat is traded for other commodities, whether calculated reciprocity is the mechanism underlying these patterns remains to be established. A simpler mechanism by which the transfer of food items could occur from a higher-ranking to a lower-ranking individual would be that any costs of interacting with a begging individual, such as reduced feeding efficiency or attracting the attention of other group members, might result in the food possessor transferring a portion of food. Infant primates have also been observed to beg for solid food from older group members (e.g., Feistner & Price 1990), and the decision of the food possessor to relinquish food will depend upon the balance between the benefits of consuming the food and the costs of ignoring begging plus any kin selection benefits. These instances of food transfer could also be described as tolerated scrounging.

The TS model is based on the difference between the costs and benefits of defending a food item. In order to differentiate between this model and reciprocal altruism (RA), it is necessary to add that tolerated scrounging occurs when the food possessor relinquishes food without the expectation of receiving food or other commodities in the future. As Gurven notes, TS could occur where the cost of not relinquishing food is a punishment, such as ostracism or a verbal or cultural sanction, and that this could result in a situation in which individuals take turns at playing the role of acquirer and recipient. This would produce a pattern of food transfers very similar to that produced by reciprocal altruism. At present, the significant contingencies reported in Gurven's Table 2 could result from TS with punishment or from RA. Gurven states that computer simulations reveal that significant correlations between amounts given and amounts received as a result of TS will occur only in highly structured groups of few individuals, but he does not give further details of these computer simulations.

Gurven proposes a number of assumptions that he suggests form the basis of the TS model. For example, Gurven suggests that food will be transferred from those with lesser need to those with greater need, that TS will not occur where the producer can control who receives food and how much, and that only powerful individuals can avoid relinquishing shares to hungry individuals. These assumptions were not part of Blurton Jones's (1987) original TS model and may not be appropriate when one considers a less restricted view of TS. Gurven also suggests that, according to the TS model, any increased demand for food, such as during a time of food shortage, should increase the breadth and/or depth of sharing. However, in these circumstances, sharing may be less likely to be tolerated if the benefits of consuming the food outweigh the costs to the food possessor of defending the item.

Knowledge of each individual's need, the level of producer control, or relative power levels will not be sufficient by itself to estimate the probability that food will be transferred; one also requires knowledge of the costs involved in defending the food item.

Key variables in tests of food sharing

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Abstract: Gurven discusses three key features of food sharing, specifically producer control, need, and contingency. I make two general points regarding the use of these variables in tests of food-sharing hypotheses. First, that these variables are relative, not absolute concepts; and second, that the predictions generated from these variables overlap significantly. In addition, I suggest frequency of sharing as a measure of contingency for the RA hypothesis.

In the long-standing debate over the function of food sharing, many of us investigating these issues in the field have come to recognize that multiple explanations are needed to account for the variety of food-sharing patterns observed among hunter-gatherer horticultural groups. Past attempts at resolving questions of food sharing have focused on testing different hypotheses, specifically costly signaling (CS), tolerated scrounging (TS), kin selection (KS), and reciprocal altruism (RA), for a single society. Gurven's approach is novel in that he looks at the various hypotheses together using multivariate models. Here he considers all the available evidence on patterns of food sharing in the ethnographic record and how this evidence plays out against the different hypotheses.

Three key features of food sharing are highlighted. For the sake of clarification I summarize below the four hypotheses for food sharing with respect to these key variables:

CS = no producer control + no need + no contingency
TS = no producer control + need + no contingency
KS = producer control + need + no contingency
RA = producer control + need + contingency

I would like to discuss two points here, the first relating to the relative nature of these key variables and a corresponding suggestion I have regarding the measurement of contingency, the second relating to the predictions generated from these variables.

First, I would like to emphasize that these key variables are relative, not absolute concepts. For example, producer control is not likely to be strictly present or absent. Control over distribution is probably more accurately considered as a range of control that may vary across time and circumstances, as Gurven acknowledges when discussing the ethnographic evidence. In addition, the absolute amount exchanged between households is likely to be a weak indicator of contingency because reciprocity should function according to marginal values (Winterhalder 1996). As such, in testing the RA hypothesis, I propose that the frequency of sharing events between households is a better measure of contingency than actual amounts exchanged. If a key component of RA is the expectation that a recipient today will return the favor in the future, then individuals may signal or reinforce their intention to cooperate by frequent episodes of sharing, even if they have little to give each time.

The second point is that the predictions generated from these key variables overlap even more than Gurven acknowledges. For instance, widespread sharing in the complete absence of producer control (or the abandonment of control that *could* exist) points clearly to costly signaling, however, TS, KS, and RA could all function together under various levels of producer control, especially if combined with strategies for non-detection to limit opportunities for tolerated scrounging. Gurven makes the statement that, "If a producer can control who receives and how much . . . then TS is unlikely to explain food transfers" (sect. 2.3). I agree that with increased producer control, TS is less likely, but it may still occur.

A hunter may not be required to relinquish all control over meat he brings back to camp, but he may still be faced with scroungers aware of his success. For such individuals with whom the hunter does not intend to share, the decision to share will then come down to marginal value for the giver and receiver, but this does not preclude intentional sharing of the same harvest with others. Especially in communities with lower visibility between households, it is possible that one scrounger becomes aware of a harvest without the entire community gaining knowledge. As long as the benefits of being a reciprocator remain greater than the benefits of being a scrounger, both strategies should be able to coexist. In other words, we might expect TS and RA to be mutually exclusive in a community if reciprocators receive no advantage over scroungers. However, if scrounging could be partially controlled through non-detection, then both types of sharing may occur, with scrounging behavior simply occurring less frequently.

There are overlapping predictions as well in terms of recipient need. Gurven discusses quantitative evidence from several groups showing that the number of consumers in a family predicts the amount the family receives from others. He concludes that recipient need is important and that this evidence is consistent with TS and RA. However, this result is also consistent with KS, because in the KS model the decision to share with a relative is determined by a cost/benefit analysis according to the equation $rB > C$ (Hamilton 1964). Thus, the more needy a relative is (or a relative's family), the more benefit he or she will receive, and the more likely the hunter is to make the decision to share with them. If the benefit is great enough, it could even account for the preferential sharing with less closely related kin.

The results of Gurven's analysis show that need and contingency are significant predictors of the amount a household shares with others. That recipient need is significant is consistent with TS, KS, and RA, but not with CS, and that contingency is significant lends support to RA. CS appears to be a special situation, and its occurrence does not necessarily show that producer control is absent, but rather, that the producer is abandoning control at that instance. As Gurven concludes, future research should focus on identifying and measuring the benefits to such costly signaling, as well as the benefits to delayed reciprocity that takes the form of social benefits. The question remains open as to when and under what specific ecological and social conditions each of these forms of sharing is most advantageous. A start to answering this question could be systematically identifying what ecological and social factors influence producer control, recipient need, and levels of contingency, or the ecological and social conditions which correspond to the prevalence of different sharing strategies.

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A kind man benefits himself – but how? Evolutionary models of human food sharing

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Abstract: Can evolutionary models explain food sharing in traditional human societies? Gurven's analysis cannot rule out any of the models (kin selection, reciprocal altruism, tolerated scrounging, costly signaling, or by-product mutualism), and quantitative partitioning of relative importance is not feasible. For now, the hypotheses seem like the proverbial blind men examining the elephant: each was partly in the right, and all were in the wrong!

Why do individuals give away valuable resources to others? Evolutionary theory, like many religions, leads one to expect that char-

itable giving will be rewarded. For example, Proverbs 11:17 in the *New International Version* of the Bible says: "A kind man benefits himself, but a cruel man brings trouble on himself." The Bible is vague about what these benefits and troubles might be. Evolutionary theory is somewhat more constrained but it also leaves open a variety of possibilities. Gurven attempts to organize the data on human food transfers and relate them to four nonexclusive evolutionary models: kin selection, reciprocal altruism, tolerated scrounging, and costly signaling.

It seems obvious that kin selection plays a role in human food transfers, because parents feed their children. However, many biologists prefer to interpret parental care of dependent offspring as maximizing individual fitness, rather than inclusive fitness. We can gloss over this accounting problem here, because Gurven focuses on giving to "other families." He points out that giving to kin is not necessarily kin selection because near neighbors might just happen to be kin. This introduces a significant technical problem: What is the appropriate null model for the distribution of food if there is no kin bias (Grafen 1990)? Gurven's path analysis of giving by Hiwi families (see Gurven's Fig. 3), which implicitly assumes a linear null model, "suggests that the positive effect of kinship on giving may be an artifact of residential distance" (sect. 7, para. 3). Gurven seems to lose interest in kin selection at this point and says no more about it, even in the conclusions. I will address the limitations of path analysis below and suggest that kin selection was abandoned prematurely.

Gurven's treatment of reciprocity does a nice job of incorporating recent thinking about asymmetrical bargaining, future discounting, trade in different currencies, and indirect reciprocity. He acknowledges that the data on human food sharing are inadequate to address indirect reciprocity. Data on direct reciprocity (Gurven's Table 2) show that in general, giving from A to B is correlated with giving from B to A, but as Gurven observes, these simple correlations are not useful for discriminating between reciprocity and something else. However, in the path analysis of Hiwi giving, which controls for distance and kinship statistically, there is a significant partial regression between family A giving to B and B giving to A. From this Gurven concludes that the evidence cannot rule out reciprocity. To be consistent, he should have also said that the evidence cannot rule out kinship.

Tolerated scrounging was recently modeled as a formal game by Stevens and Stephens (2002), who showed that each player's alternatives are as important as the relative value of the resource. From the game-theoretic perspective, tolerated scrounging is an odd sort of mutualism where the harassing scrounger has manipulated the payoffs so that it is in the immediate best interest of the resource holder to share a little. The data on tolerated scrounging are inadequate for a path analysis. Gurven assesses the necessary condition of donor control and concludes that this mechanism seems overstated. However, the evidence cannot entirely eliminate tolerated scrounging.

Costly signaling could be treated as a component of indirect reciprocity because it acts through an audience. Gurven separates it because many anthropologists are interested in the mating benefits of food sharing. Sexually selected food sharing means that we need to identify giving by different sex and age groups. The data do not support a path analysis. Gurven surveys some case studies and concludes that costly signaling may be "a relevant yet narrow influence." However, we cannot conclude that this influence is smaller than the others until we have some quantitative measures of variance and effect size in an integrated multivariate analysis.

By-product mutualism (Dugatkin 1997) is not given category status by Gurven, but he does mention relevant issues such as defense against enemies and the possibility of individuals moving among bands. Common enemies give competitive neighbors mutual interests (Getty 1987), and the possibility of neighbors switching to enemy bands sets the stage for negotiations like those addressed in the literature on reproductive skew and group augmentation (Reeve & Jeanne 2003). Dugatkin (1997, p. 6) provides a nice quote from Darwin's *The Descent of Man,* about the importance of a tribe having a great number of courageous, faithful members to defend each other and conquer other tribes. If intergroup conflict was as important in human history as we think, it might have selected for food sharing as a form of team-building. The evidence cannot rule out by-product mutualism.

Path analysis seems like a promising way to get quantitative estimates of the relative importance of the various nonexclusive hypotheses. However, there are many possible alternative path models for any given system of variables, and the path coefficients for any particular model are not reliable estimates of the actual importance of the different variables. For example, the path coefficients in Gurven's Figure 3 might suggest that relatedness is only two-thirds as important as distance in determining giving, but this would not be a safe conclusion. Alternative models, for instance with the positions of relatedness and distance switched, would give different numbers. Path analyses can be useful if they are interpreted cautiously, but they will not reliably partition variance across different "causes" (Mitchell 2001).

My assessment is that kin selection was abandoned prematurely. Reciprocity cannot be ruled out. Tolerated scrounging might be overstated but it cannot be ruled out. Costly signaling remains relevant. By-product mutualism is potentially very important. We started with four evolutionary hypotheses for how a kind man benefits himself and we ended up with five. This does not look like progress from the perspective of strong inference, but these hypotheses are neither mutually exclusive nor exhaustive, and strong inference is a naïve standard. Path analysis is a potentially useful approach to partitioning relative importance, if adequate data can be developed. For now, the hypotheses seem like the proverbial blind men examining the elephant from different perspectives: each was partly in the right, and all were in the wrong!

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The purpose of exchange helps shape the mode of exchange

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Abstract: In his state-of-the-art review, Gurven compares evolutionary theories of food transfers in ethnographic settings. Although this is useful, I suggest that one must first try to determine the utility of food transfers before making predictions about which parties ought to receive food. In addition, I argue that tests of kin selection theory present a special problem in food transfers.

When many of us first began to investigate the utility of using evolutionary approaches (largely kin selection and reciprocal altruism) to investigate food transfers in the mid-eighties, we optimistically assumed that we could successfully defeat Sahlins's (1976) claim that patterns of cooperation and food sharing could not be predicted by the biological facts of relatedness or reciprocal altruism. Behavioral ecological theory caused major changes in field methods by evolutionarily inspired economic anthropologists. We began to quantify, for the first time, flows of food resources and labor between households and individuals. As Gurven demonstrates, there is still reason for optimism even if issues have proven more complex and far richer than we first anticipated.

Before one begins testing food transfer models such as kin selection (KS) or reciprocal altruism (RA), I suggest that one needs to deal with a prior problem of whether to share at all. That is, why is it adaptive to exchange in the first place? After we answer that

question, our choices of models to employ will be constrained. Among the Ache, for example, it appears that high variance in large game returns coupled with the adaptive value of low variance in food consumption sets the stage for exchange. Game in the optimal diet breadth has many high-yield but high-variance targets so that one may go several days without capturing sufficient game to meet the dietary needs of a hunter's family. As Kaplan and Hill (1984; Kaplan et al. 1985) show, sharing among hunters provides a solution to the problem by reducing the variance across hunters through pooling risk. The Ache perhaps could solve the problem of high variance by targeting smaller game whose return is less variable. However, the cost of doing so would lead to a nonoptimal diet breadth for a simple reason: hunters would not pursue risky game with higher long-term rates of return, thereby reducing their overall rate of return while hunting.

Given that sharing provides a means to reduce variance in intake, then the next problem to solve is how many and what kinds of individuals you need in a sharing coalition to reduce variance to an acceptable level (a problem mathematically modeled by Winterhalder 1986). The smaller the number of sharers, the better – for one thereby reduces the problem of free riders. As it turns out for the Ache, the number shared with is the same as the number of hunters and their families in a band. It may be the case that band size is adjusted to reflect this number. I would argue that RA is the only reasonable model to apply to this situation. So long as all hunters are making earnest efforts, one could not divert larger than equal portions to kin because one needs to depend on a greater number of hunters than found among close kin. Furthermore, favoring kin would cause the system to disintegrate because the pool necessary to reduce variance would be too small. Such a system does not rule out the possibility of especially proficient hunters from expending additional efforts as in the costly signaling (CS) model outlined by Gurven. However, it appears that CS or good hunters gaining extra-pair copulations (Kaplan & Hill 1984) seems decidedly secondary in such a situation.

There are undoubtedly any number of adaptive reasons for sharing, aside from variance reduction. As Gurven points out, in numerous cases cooperative acquisition leads to RA, and biasing kin would wreck a system of efficient group acquisition. In other instances, secondary food transfer to needy kin (e.g., young families with high consumer-to-producer ratios) in the context of RA variance reduction systems may be adaptive as long as the costs to one's fitness are less than the benefit to kin.

KS models will prove difficult to test, and Gurven does not provide us with insights on how we may evaluate such models. The classic KS model is dyadic in form, but humans live in families, and much more often than not food is given to other families and not individuals. This leads to a problem of how one calculates relatedness, and to what I have referred to previously as the targeting problem (Hames 1987). If a woman decides to give food to another family, does one measure the relatedness between the woman and her sister to whom she gives the food, or the woman's total or mean relatedness to other members of her sister's family? This issue is complicated by the fact that although one may give food to a family, one has no way of determining who in that family will ultimately consume the food.

In section 4.2 Gurven deals with the issue of whether food flows according to need. That is, do people who have an easy time making ends meet, provide food to families that are unable to feed themselves adequately. His review of the literature leads him to conclude that there seems to be considerable pressure on successful producers to share their largesse with those less fortunate and they "may receive prestige, support, or social insurance" in doing so. I agree. However, he fails to recognize that I tested (Hames 2000, Table 3) a need-based egalitarian model of food exchange whereby food should flow from households with low consumer-to-producer ratios to those with high consumer-to-producer ratios. It did not. Instead, what I did find, as Gurven notes (Table 2 of the target article), is moderately strong support for RA among the Yanomamö.

Furthermore, in the same section (sect. 4.3) and later in Gurven's analysis of Hiwi food flows, family need is measured by the number of consumers. I would think that a consumer-to-producer ratio is a much better measure of need. Imagine two families of five with two reproductive adults in each, but one has three children older than 16 years whereas the other has three under the age of 10. As Kaplan (1994) and Kramer (2002) demonstrate for horticultural groups, young children consume more than they produce and that production does not equal consumption until after the age of 16. Consumer-to-producer ratios are a much more sensitive measure of need or productive capacity than family size.

Despite these critiques, Gurven has produced the best overview of patterns of food transfers in traditional societies and a reasoned assessment of the models that attempt to account for them. As Gurven shows, it is apparent that not all food is the same and that even within a particular group multiple models may be supported. He importantly recognizes that we need to get a better idea of the moral systems that regulate food transfers, an important dimension of transfer theory that has long been neglected and has the potential to unite the behavioral economic literature (Henrich et al. 2001a) on cooperation with behavioral ecology.

On sharing a pie: Modeling costly prosocial behavior

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Abstract: In this comment, I describe how the processes of free giving can be simulated with the help of the Reflexive Intentional Model of the Subject (RIMS). This simulation demonstrates that there are two essential factors affecting the size of a share given to others: limits accepted by the society as "normal," and the individual's subjective estimation of a mean share donated by other members of the society.

In his article, Gurven mentions that costly prosocial behavior is viewed by many researchers as "anomalous" because it violates the "axiom of rationality." This axiom underlies the majority of formal models of economic behavior, resulting in difficulties of using them for representing the situations in which "individuals give valuable resources away to others." Within the last decade, a new model has been developed, the Reflexive Intentional Model of the Subject (RIMS), which allows us to include into consideration, in addition to economic factors, the subject's prestige and his ability to make bipolar moral evaluations (Adams-Webber 1997; Krylov 1994; Lefebvre 1992; 2001; Miller & Sulcoski 1999). Among other uses, RIMS is employed for modeling terrorist activity (Kaiser & Schmidt 2003). I will show below how RIMS can be used for modeling the processes of products' distribution.

Let a subject have the task of cutting a pie in two parts: one for himself and the other to give away. Let the subject's social status depend on the pie share he takes: the smaller the share, the higher the status. (I have to note that this assumption is not universal. For example, in contemporary Russian and German cultures, one's offering too big a "pie share" to another person may be considered a sign of mockery or challenge. I will return to this later.) Let two types of subjects exist. For the first type, social status is the most important value; for the second type, the pie itself is the dominant value. The latter would increase his share even at the cost of losing his social status. Note that the situation described is not an ultimate game (see, e.g., Fehr & Gachter 2000), because the subject is not punished economically if others reject his giving.

I will now describe a simple procedure of pie sharing based on RIMS. This model can be used in such situations as when the subject distributes a product between two "agencies" under the condition that giving the product to one agency is considered by the subject as a positive action, and giving it to the other agency as a

negative action. In the simplest case, the share related to the positive action is represented with the following equation:

$$X_1 = x_1 + (1 - x_1)(1 - x_2)x_3, \quad (1)$$

where x_1,x_2,x_3 belong to interval [0,1] (Lefebvre 1992). The value of X_1 is the share which the subject is *ready* to give to the positive agency; x_3 is the share which the subject has *intention* to give, that is, the share he would give to the positive agency if no external factors influence him; x_1 is the pressure of the close environment inclining the subject to give the entire pie to the positive agency, and x_2 is the subject's evaluation of the normative pressure.

The model represented by equation (1) allows formal definition of the subject's state in which he is capable of making an *intentional choice.* This state corresponds to an additional limitation $X_1 = x_3$. In this case the subject's readiness coincides with his intention, and variable X_1 can be eliminated:

$$x_3 = x_1/(x_1 + x_2 - x_1x_2), \quad (2)$$

where $x_1 + x_2 > 0$.

One of the agencies to which the subject distributes the pie shares can be the subject himself, and the other one, other people. For the subject of the first type, the one who cares about his social status, the positive action is *to give,* and the negative action is *to not give.* For the subject of the second type, who prefers the pie to the status, the positive action is *to not give,* and the negative action is *to give.* I begin with modeling the first type of subject. The value of x_3 in equation (2) is the share of pie which this subject intends to give to the others. I assume that the larger the share the subject intends to give to others, the less the pressure from the environment on him: $x_1 = 1 - x_3$. Besides the closest surroundings, information about the "larger" society also influences the subject. He has some view of what share other people usually give away; I designate it x*. Then, the individual's subjective estimation of the normative pressure is $x_2 = 1 - x^*$. After substitution of these values for x_1 and x_2 and transformation, I obtain the following equation:

$$x_3 = 1/(1 + \mathrm{SQRT}[1 - x^*]) \quad (3)$$

It follows from equation (3) that the share which the subject will give away depends only on x*, that is, on the share given by other members of the society, from the subject's point of view. For example, if $x^* = 1$, that is, from the subject's point of view, other people offer up the entire "pie," the subject will also donate the entire "pie" ($x_3 = 1$). If, from his point of view, the others do not give at all, $x^* = 0$, the subject will donate half of the pie ($x_3 = 1/2$).

Consider now the subject of the second type. The value of x_3 in equation (2) corresponds to the share that the subject intends to take. Considerations similar to the one given above leads us back to equation (3), where x* is the share that, from the subject's point of view, other people take themselves. If $x^* = 1$, that is, the others take the entire pie, then $x_3 = 1$, the subject also takes the entire pie; if $x^* = 0$, that is, the others, from the subject's point of view, offer up the entire pie, the subject will offer up one half of the pie ($x_3 = 1/2$).

If the subject does not know the pressure applied to other people, the normative pressure is equal to the pressure he experiences, and we have to assume $x_1 = x_2 = 1 - x_3$. After substituting these values in equation (1) and applying condition $X_1 = x_3$, I obtain the following cubic equation:

$$x_3^3 - 2x_3 + 1 = 0. \quad (4)$$

Two roots out of the three belong to interval [0,1]: $x_3^{(1)} = 1$ and $x_3^{(2)} = (\mathrm{SQRT}(5) - 1)/2 = 0.618\ldots$. The second root is the golden section value. Thus, the model predicts that in this case, the subject gives either the entire pie to the positive agency or the part of it equal to the golden section value.

In conclusion, I will consider a problem of pie sharing from the more general point of view. We know that in the large modern societies, there are limits within which product distribution is considered "normal." For example, if after winning $20,000 in a lottery, a person gives away everything to the first comer or escapes without paying taxes, his behavior is considered insane or criminal. To reflect these limits in a formal model, I introduce values P_{max} and P_{min}. Then the size of the pie analyzed earlier is:

$$S = P_{max} - P_{min}. \quad (5)$$

Under certain circumstances, equation $P_{max} = P_{min}$ may hold; this means that the society completely determines how to share the product. For example, $P_{max} = P_{min} = 1/2$ means that the society dictates that its member should share the product in two equal parts.

The history of human food transfers: Tinbergen's other question

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Abstract: Emphasis on cross-cultural testing, multiple currencies, multivariate analyses, and levels of explanation makes this an important paper. However, it does not distinguish current function from evolutionary origin; it lacks history. Rather than distinct alternatives, tolerated scrounging (TS), costly signaling (CS), and reciprocal altruism (RA) are likely to be sequentially evolved components of a single integrated system (and kin selection (KS) important only among very close relatives).

Tinbergen famously described four ways to ask "why" with respect to any biological trait. What is its survival/reproductive value (function); what proximate factors make it happen (causation); how, in the course of an individual's life, does it come to be (development); and finally, how, in the course of phylogenetic history, did the three preceding factors come together to produce the trait we see (evolutionary history)?

Gurven has made a valuable contribution to the first of these questions and has touched on excellent evolutionary psychological approaches to at least some elements of the second (e.g., Henrich et al. 2001b). The third is largely ignored (though implicit in cross-cultural work), but the real danger is that readers will take from his analysis of contemporary function the idea that evolutionary history has been addressed. Gurven concludes (sect. 9, "Conclusion," para. 2) that "[s]ome of the difficulties in understanding sharing behavior stem from a confounding of the levels of analysis: proximate motivations, cultural prosocial norms that partially correlate with actual behavior, and outcomes in terms of genetic fitness." He is absolutely correct, and this is an important point, but he addresses only the first three of Tinbergen's questions. The general problem of confusing function and history is not new; the spandrels of San Marcos are well known to behavioral ecologists.

The problem is that efforts to model the evolution of reciprocal altruism (RA) always have difficulty with getting it started. Once RA is established in a population sub-unit, it is not hard to see that noble band of non-brothers winning out; within that first group, though, one must appeal to failed kin recognition or some similar *deus ex machina* to overcome the initial disadvantage of being a lone altruist. One approach has been to argue that altruism is not altruistic; in the case of food sharing, it is not difficult to (conceptually) evolve tolerated scrounging (TS) and/or costly signaling (CS) via individual selection (and kin selection [KS] is not a theoretical problem, though it may be an empirical one [Moore 1992]). The problem is that humans are clearly capable of real, genuine altruism that just does not fit KS, TS, or CS predictions. As Gurven points out, at present none of the models can be eliminated, and this leaves us with three logical alternatives. Further evidence will exclude one or more; two or more evolved independently, are not proximately connected, and only seem similar; or finally, two

or more evolved sequentially and represent contingent aspects of an evolutionarily integrated behavioral package.

Gurven does not consider the last possibility, so one is left with the second, "mixed salad" approach to account for available data. This is eminently sensible when attempting to explain modern behavior: Is a given action or norm based more in RA or CS? However, postulating evolutionary independence for such similar-appearing behaviors is not parsimonious and leaves us still with the difficult task of explaining the evolution of RA. Furthermore, the analytical separation of the models needed to generate testable predictions tends to exaggerate differences between them, resulting in, for example, a caricature of TS (sects. 3.1–3.2) in which "producers have little to no control over who receives shares" but instead food flow is distributed according to relative need, "[a]ssuming equal ability to defend resources." The statement that "TS asserts that only relative need and power should have any influence on the direction of food transfer" is true only if need and power are defined circularly (the one who got it was neediest and most powerful), as embodied in the saying that possession is nine-tenths of the law. TS works at the margin of that last tenth.

I suggest instead that TS, CS, and RA are functionally and historically related, having developed in that order during hominin evolution. In brief, postulate a resource that has high nutritional value, is difficult to acquire, is portable once obtained, and when obtained often comes in packages large enough and ephemeral enough that an individual holder's marginal utility is likely to approach zero before it is fully consumed. Meat in the form of monkey-sized carcasses (roughly, 5–15 kg) is an obvious possibility, though not the only one (e.g., some tubers). As pointed out by Wrangham (1975) with reference to chimpanzee hunting, the holder of such a resource is unlikely to be able to eat anything until scroungers are "bought off" with shares; this is TS.

However, this is not the end of it; TS creates its own social relationships in which holders can exert influence over scroungers. A holder may not be able to keep it all, but can bias its distribution and can either give readily or make scroungers beg intensely (donating minimal bits just before the interaction escalates to a costly attack). In other words, the resource becomes a social tool, and the stage is set for the psychological mechanisms underlying CS to evolve. TS is not replaced, it is added to, and TS/CS exist in a dynamic tension – scroungers scrounge for valuable bits of resource (TS), but in doing so must "pay" in social standing (CS). Finally, in this story, the ability to engage in RA can evolve as essentially a sociopolitical modification of the TS/CS complex in which individuals alternate scrounger and holder roles, motivated by a desire to even the CS-based social score (cf. Mauss 1925/1967).

This scenario has the advantages of accounting (roughly) for the origin of RA without relying on luck, being somewhat more parsimonious than the multiple-origin story, and fitting Gurven's data with very few loose ends. It has the marked disadvantage of not easily generating clearly distinct hypotheses, because it holds that the models themselves are interlinked and contingently enacted. Sometimes life is like that, and we can only hope that the approach taken by Henrich and others will untangle the knot. For full explication of the story, see Moore (1984; available at http://weber.ucsd.edu/~jmoore/publications/Recip.html).

Incidentally, the statement that "[f]ood production, or allocation to the public good, is thus viewed as a collective action problem because nonproducers consume portions without paying any production costs" (sect. 3.3, para. 3) coupled with TS/CS suggests an explanation for the puzzle of why humans apparently did not adopt agriculture until forced to do so by population pressure (cf. Cohen 1977).

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The complexity of human sharing

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Abstract: Although an excellent review, the target article displays a bias in favor of reciprocity-based explanations and against alternatives. Tolerated scrounging is more subtle and pervasive than portrayed here. Costly signaling need not be limited to public displays and generalized sharing. The theoretical basis for extensive sharing and other forms of collective action remains unresolved, and standard reciprocity-based explanations are insufficient.

By reviewing and critiquing important evidence and theory bearing on food sharing in small-scale human societies, Gurven has provided a valuable service. As his account demonstrates, this is an area characterized by unusually diligent quantitative research, sophisticated theory, and active debate over competing explanations – hallmarks of the relatively small but active field of human behavioral ecology (Winterhalder & Smith 2000). The critical comments that follow are meant to stimulate further research and theory development, and if they concentrate on certain weaknesses in Gurven's account, this is by no means to question the overall quality and value of the paper.

Despite Gurven's avowed intention to consider all hypotheses on an equal basis, I detect a bias in favor of reciprocity-based hypotheses. For example, after noting that evidence supports the hypothesis that large game transfers among the Meriam and the Hadza depend on tolerated scrounging (TS), he argues that this is only part of the story "[i]f the Meriam reciprocally share yams, bananas, and chicken, or if the Hadza reciprocally share roots and small game" (sect. 1, last para.). But there is no evidence that these "ifs" have any basis in fact, and raising these counterfactuals is likely to mislead non-specialists.

Gurven's representation of TS has other problems. He argues that "If a producer can control who receives and how much, or if marginal value is linear or increasing (as a result of trade, for example), then TS is unlikely to explain food transfers" (sect. 2.3, para. 1). This statement is misleading at best. First, control over one's own production is actually necessary for TS, because TS is based on the trade-off between the cost of defending all of the product versus relinquishing some of it to scroungers; if there is no control at all, then consumption should simply involve scramble competition. By "control," perhaps Gurven means complete producer choice over the recipients of food transfers, but even under pure TS a producer could influence this variable by choice of when and where to forage, or by pre-empting the demands of some by sharing with others. Second, diminishing marginal value is a necessary condition for TS only if the marginal costs of resource defense equal the marginal costs of scrounging (as determined by the relative "resource holding potential" [RHP] of producer and scrounger). There is no reason to expect RHP to be equal in all potential producer-scrounger relations.

Gurven makes little mention of the extensive theoretical and empirical work on producer-scrounger interactions in the animal behavior literature (e.g., Beauchamp & Giraldeau 1997; Giraldeau & Caraco 2000). This literature is important for showing how pervasive and evolutionarily stable TS is in other social species. I would never argue that TS is the dominant form of food transfer in human foraging economies; but it may apply to a wider range of conditions than Gurven suggests. Even when technically absent, its *potential* for being exercised may motivate other forms of food transfer more profitable to the producer. This is in fact the scenario suggested by the originator of the TS model (Blurton Jones 1987).

Turning to costly signaling (CS), I question the statement that "the payoffs to signaling derive only from the honest display of production to a wide audience, and not from giving to specific individuals" (sect. 3.2, last para.). This conflates particular cases or

applications of CS with the broader explanatory purview of this framework. Despite the emphasis my colleagues and I have given it, the wide-broadcast extensive-sharing form that characterizes Meriam turtle hunting and feast provisioning should not be taken as the only (or even necessarily the primary) way CS can influence food transfers. Even in the Meriam case, spear-fishing – which involves very little food transfer but considerable display – is an equally good example of CS (Bliege Bird et al. 2001). Every time one sends a birthday gift to a friend or relative, invites a colleague over for dinner, or bestows an engagement ring on a beloved, one is engaging in a form of "giving to specific individuals" that likely has a strong or dominant CS component. Although applications of CS to hunter-gatherer food sharing have to date emphasized big game and wide broadcast, this is certainly not inherent in the model.

I do not understand the basis of Gurven's claim that the existence of enforced norms to share and to produce "eliminates the collective action or public goods problem of group food production decisions" (sect. 4.4, para. 4) as well as the second-order problem of norm enforcement. Theory shows that norm enforcement is a second-order collective-action problem, although at high frequency of first-order cooperation there is little cost to being an enforcer (Boyd et al. 2003). To date, the only theoretically viable solutions to the second-order problem are cultural or genetic group selection (Bowles et al. 2003; Henrich and Boyd 2001), political inequality with differential gains to enforcement (e.g., Ruttan & Borgerhoff Mulder 1999), and costly signaling (Gintis et al. 2001; Smith & Bliege Bird 2000b).

To emphasize my earlier point that the target article is an excellent contribution, let me close on a positive note. Gurven notes that "although signaling generosity is costly in the short-term, long-term benefits may accrue in societies where there are frequent opportunities for cooperative gain, when payoffs to cooperation at these opportunities are substantial, and when the choice of cooperative partners is based on observations of past generosity" (sect. 9, para. 2). Recent theory (Gintis et al. 2001; Lotem et al. 2002; Mohtashemi & Mui 2003; Panchanathan & Boyd 2003) and experimental evidence (Milinski et al. 2002; Semmann et al., in press) strongly support this view and reinforce the ethnographic evidence cited by Gurven. Indeed, there is no need to limit the source of information about past generosity to direct observation. It seems increasingly likely that the elaboration of group-beneficial cooperation in humans, which remains one of the outstanding challenges to modern evolutionary analysis, may be driven to a considerable degree by the reputation-building amplification offered by linguistic communication, especially when combined with the greatly expanded opportunities for group production created by our species' technological and cultural capabilities (Smith 2003).

Insights from Ifaluk

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Abstract: The fish-sharing patterns on Ifaluk Atoll underscore several limitations of the explanations of food sharing offered by Gurven and suggest that non-foraging labor activities may provide insights into reciprocity and punishment relevant for understanding food-sharing patterns. I also argue that future food-sharing studies should focus on signaling rather than resource holding potential (RHP).

Michael Gurven is to be commended for his thorough review of the anthropological food-sharing literature. Gurven has introduced a vocabulary (depth, breadth, balance, etc.) into the food-sharing literature that will encourage additional systematic analyses and further enable us to make cross-cultural comparisons using standardized measures. The interrelationship between these variables highlights the trade-offs that individuals face when they consider transferring food items. Understanding the selective pressures that have shaped the psychology of food-sharing decisions should clarify the value of each of the measures that Gurven introduces.

Although I am largely in agreement with Gurven's theoretical positions, there is some confusion in the target article concerning how to understand trade, which Gurven considers "a form of RA in which the products given and received are in different currencies" (sect. 2.2, para. 1). Reciprocal altruism (RA) offers a potential explanation for the short-term behavioral costs of giving resources to another organism: namely, these costs will be compensated by future gains. Trade does not entail short-term behavioral costs but refers to transactions in which the currency and quantity may be negotiated. Once an agreement is reached there is generally no delay between exchanges of items, which is a critical element of RA. When there is a delay in a trade exchange, the delay is usually supported by a formal or informal contractual agreement, unlike RA. Hence, trade should be analyzed as a distinct form of exchange and not as a subcategory of RA.

Despite the focus in the target article on kin selection (KS), tolerated scrounging (TS), reciprocal altruism (RA), and costly signaling (CS), food-sharing patterns in some populations may require alternative explanations. The sharing of fish on Ifaluk is an instructive example. Ifaluk fishers have little to no control over where the fish they cooperatively catch are initially distributed. An individual whose authority was inherited from his matriline determines who receives fish and the amount they receive. KS, TS, RA, or CS cannot explain why Ifaluk fishers willingly allow someone with an inherited position to determine where their catch goes. Nor can these theories explain how the culturally sanctioned distribution patterns emerged on Ifaluk and why they are maintained. Some of these patterns differ considerably from any patterns described in the target article, such as distributions based on land ownership in which the size of landholdings entitles owners to a specific percentage of the harvest (Sosis 2000b).

Although other models may be necessary to explain the specific cultural patterns which emerged on Ifaluk, mutualism offers the most likely explanation for why Ifaluk fishers share their harvest at all. When resources are acquired through the mutual coordination of multiple individuals, it is often difficult to assign responsibility for a unit of the harvest (Alvard & Nolin 2002). Cooperative fishing on Ifaluk requires such coordinated effort; whether rowing, steering, pushing the mast, or reeling in fish, every role is vital for success, and hence no single individual can claim ownership of any particular fish. When fish are captured through solitary means and ownership is unambiguous, fish are shared much less extensively (Sosis 2001). A comparison of atolls in the region supports the importance of mutualism in maintaining food-sharing patterns on Ifaluk. In contrast to neighboring atolls, Ifaluk chiefs have forbidden the use or ownership of motorboats. When motorboats were introduced to Ifaluk's neighbors, the traditional sharing systems of these atolls collapsed. With motorboats men no longer needed mutual cooperation to capture fish and they consequently maintained control over their catch, sharing only within their nuclear family. While mutualism can probably explain why Ifaluk fishers relinquish control of their catch, it should be noted that KS, TS, CS, and RA are likely to be important in explaining secondary distributions on Ifaluk (i.e., fish that are further distributed by families after the distributor initially distributes the harvest), although analyses have yet to test these hypotheses rigorously.

On Ifaluk men do not have control over the fish they capture cooperatively; however, as Gurven notes, producer control is less clear in other foraging societies. Indeed, this ambiguity has generated considerable debate among behavioral ecologists concerning the possibility of TS (Hawkes 1993; Hill & Kaplan 1993). One avenue out of the debate may be to model food transfers as a sig-

naling problem rather than a resource holding potential (RHP) problem. As Gurven mentions, RHP has not been measured for any human population. Interactants attain knowledge of RHP through signaling; hence we may be better off focusing our attention on the signals rather than on actual RHP. Common experiences with fund-raising appeals underscore the importance of signaling in understanding TS. We are likely to forgo some of our wealth (which there is no debate that we control), not to those who are necessarily the most in need, but to those solicitors who send the most persistent signals and are able to impose the highest reputational costs on us by signaling to others. Indeed, the most destitute individuals are often incapable of sending an influential signal that can motivate us to contribute to their cause because they lack the resources to maintain our attention or impact our reputation.

Gurven correctly notes that future work on food sharing will need to examine the relationship between production, consumption, and punishment. There are two types of tangible punishments for slackers that occur on Ifaluk, which I add to the list of punishments offered by Gurven. First, the distributor may bias distributions away from those men who repeatedly do not fish. As in many societies, larger harvests on Ifaluk are widely distributed to all members of the community. However, when some men repeatedly failed to fish, the distributor gave these large harvests to those compounds that owned the canoes that caught the fish; that is, those who did not participate in the catch did not receive fish. Second, a reputation as a slacker resulted in an inability to generate assistance in other cooperative tasks on Ifaluk. For example, roofs are rethatched on Ifaluk huts about every two years. Prior to a rethatching event, the chief announces that all adult males should bring a certain number of woven coconut fronds (dependent on the size of the house) for rethatching on a certain day. Men who do not regularly contribute to cooperative fishing efforts have difficulty getting men to contribute thatch or show up to rethatch the roof. One notable shirker was forced to put a plastic tarp on his roof because he was unable to get the help he needed. This punishment highlights the need for research which looks comprehensively at foragers' labor activities, because they may provide data on trade, reciprocity, and even punishment that could explain otherwise puzzling sharing behavior.

Cognitive constraints on reciprocity and tolerated scrounging

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Abstract: Each of the food-sharing models that Gurven considers demands unique cognitive capacities. Reciprocal altruism, in particular, requires a suite of complex abilities not required by alternatives such as tolerated scrounging. Integrating cognitive constraints with comparative data from other species can illuminate the adaptive benefits of food sharing in humans.

Gurven argues that reciprocal altruism (RA) provides the best adaptive account of human food sharing, explaining the patterns better than tolerated scrounging (TS), kin selection, and costly signaling. We contend that the emphasis on RA may be overstated, whereas the analysis of TS is overly critical. To address the overemphasis on RA, we make the following argument: First, a more recent model of TS situations avoids the specific assumptions and predictions of previous models, providing a more generally applicable version of TS. Second, the presence of contingency is not sufficient to invoke RA, because confounding factors can produce reciprocal patterns. Third, using a comparative approach, we argue that RA rarely occurs in nonhuman animals, probably because of the complex cognitive skills required to reciprocate. Given these cognitive constraints, we examine the adaptive history of human food sharing originating from TS situations. In total, these contentions suggest that, minimally, TS provides as reasonable an explanation of the available data on human food sharing as RA does.

Gurven adopts a strict definition of TS. Although the previous optimality models of TS considered by Gurven require special circumstances and make overly specific predictions (Blurton Jones 1984; Winterhalder 1996a), a recent model of TS based on more general assumptions does not predict egalitarian food sharing (Stevens & Stephens 2002). This model predicts that if the beggar's harassment is costly enough to the owner, the owner may relinquish a fraction of the food to the beggar to avoid these costs. The optimal amount shared depends on the costs of harassment to the owner and to the beggar, as well as the consumption rate of the consumers, so equal distribution of the food is unlikely. In contrast to the original TS formulation, in the Stevens and Stephens model the food owners can control the distribution of the food and the marginal value does not have to decrease. Therefore, many of Gurven's assumptions and predictions for the TS model do not apply to the more general harassment model.

In contrast to his strict view of TS, Gurven uses very relaxed criteria for RA. His crucial evidence for RA is the contingency of giving – individual A's sharing with B correlates with B's sharing with A. This type of analysis is necessary but not sufficient to assess contingency because of potential confounding factors such as association. Rather than being contingent on previous instances, sharing may result from associational relationships between individuals (de Waal & Luttrell 1988); that is, individuals who interact frequently for any reason, tend to demonstrate reciprocal sharing patterns. Moreover, repeated, reciprocal TS interactions could lead to patterns of sharing identical to RA. Therefore, examining long-term patterns of contingency alone cannot provide the resolution to distinguish between RA and repeated TS interactions. Gurven is clearly aware of these issues, but much of the available data does not allow him to test between these alternative hypotheses.

The distinction between RA and TS is further complicated by Gurven's inclusion of punishment with RA. Theoretical investigations of reciprocal altruism suggest that punishment and social norms may play a critical role in maintaining cooperative behavior (Boyd et al. 2003; Gintis 2000). And indeed, Gurven's survey of the literature reveals that punishment and coercion regularly occur in hunter-gatherer societies. As Gurven himself points out, however, "the resulting 'reciprocal' TS . . . is essentially identical to RA" (sect. 8.3, para. 1). In light of this convergence, how do we distinguish between the two hypotheses?

Because the present view of human food sharing – one enforced by social norms and punishment – is equally compatible with TS and RA models, we examine the probability that each model accounts for the adaptive history of food sharing. Comparative data suggest that the cognitive constraints on RA pose a substantial barrier to its evolution (Stevens & Hauser 2004), whereas the considerably more relaxed constraints on TS make it a likely candidate to explain present behaviors. In addition, empirical support for RA is virtually nonexistent in nonhuman animals (Hammerstein 2003). Even in the few cases that report RA, such as vampire bats (Wilkinson 1984) and primates (Brosnan & de Waal 2002), it either is rare or requires special conditions (Hauser et al. 2003; Stephens et al. 2002). Evidence for TS and harassment, however, is much more common among animals (Clutton-Brock & Parker 1995; Stevens & Gilby, in press).

Why might reciprocity rarely occur and harassment commonly occur in animals? An important difference between RA and TS is the timescale over which the costs and benefits accrue. RA implies that an individual pays an immediate cost to share and waits a period of time before recouping that cost, presenting at least two barriers to cooperation. First, animals (including humans) prefer immediate over future benefits, and, therefore, devalue future re-

wards. As Gurven points out, discounting has important consequences in cooperative interactions (Rachlin 2002). Individuals who highly discount future rewards may have difficulty employing reciprocal sharing strategies. Second, introducing a time delay requires that individuals remember that they owe a debt or have given a favor to another, and remember the amount of that debt or favor. Memory decay and interference can make tracking debts and favors difficult. The presence of a time delay allows for interactions with multiple individuals, further increasing the cognitive load by requiring simultaneous tracking of interactions with several partners. For these reasons, the probability of sharing should be inversely related to the expected reciprocation time.

TS strategies do not suffer from the same limitations because the benefit to the harasser accrues immediately. Whereas RA demands the evolution of a cognitively taxing strategy, harassment demands the evolution of a relatively simpler strategy in which selfish instincts result in immediate rewards. Implementing repeated TS strategies not only superficially resembles RA, but may pave the way for RA by introducing a behavioral repertoire of enforced social norms on which stable RA strategies ultimately depend (Blurton Jones 1984).

The argument from cognitive constraints is not designed to be a knock-down punch, nor do we expect that any single model will stand alone in the final rounds. Like Gurven, we suspect that elements of each of these models may be at play in the context of human food sharing. It would be a mistake, however, to broadly construe the predictions of RA while narrowly confining the predictions of alternative hypotheses to a restricted set. Existing evidence of food sharing is equally compatible with the harassment model of TS, and the lower cognitive demands of harassment favor it as an adaptive hypothesis.

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The details of food-sharing interactions – their cost in social prestige

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Abstract: I agree with Gurven that costly signaling can explain food-sharing phenomena. However, costly signaling may also explain the role of food sharing in deterring rivals. Details of food-sharing interactions may reveal gains and losses in the social prestige of the interacting parties. The evolutionary models of kin selection and of reciprocal altruism are unstable and should be avoided.

Gurven omits models of group selection (GS) from his discussion of the adaptive significance of food sharing. He does so for a good reason: not because the data do not fit models of GS, but because of the general agreement among most sociobiologists that GS models are vulnerable to social parasitism. Yet, Gurven considers models of kin selection (KS) and of reciprocal altruism (RA) to explain the phenomena of food sharing. But KS and RA are just as open to social parasites as is GS (Zahavi 1995). An individual in a kin group may benefit from the investment of his other kin in the kin group without investing in the good of his kin himself. This is precisely the argument because of which GS was discarded as an unstable model. The sharing of food between parents and their offspring of all generations has nothing to do with KS models, because such sharing can be explained by the direct advantage to the fitness of the parent through simple individual selection.

All forms of RA suffer from instability as well. Without enforcement, RA is open to social parasites. But enforcement of reciprocation entails an investment on the part of those who enforce reciprocation or discriminate against the social parasites. Why should one bother to act as police or to impose a grudge if others are already doing that? Thus, the very mechanism that ensures reciprocation in RA models demands as much of an explanation as the problem of altruism that RA was supposed to solve in the first place.

Treating trade as a form of RA is mixing a simple utilitarian phenomenon with altruism; the case of the trading of honey for deference is a case of costly signaling (CS) rather than of RA.

The fact that food is often shared among kin is not necessarily evidence that KS was the mechanism that selected it. Likewise, reciprocal sharing of food is not necessarily evidence that it has evolved because of the mechanism of RA.

Unlike KS and RA, which are both models of indirect selection, tolerated scrounging (TS) is a simple, stable model based on individual selection. Both the recipient and the donor gain: The recipient gets the food and the donor saves the effort of defending food that may not be defendable or is not worth defending. CS models are also based on direct benefit to the donor and hence are stable models (Zahavi 1995).

Food transfer (allofeeding) occurs also among birds. It often occurs in courtship, but is also common among adults of the same gender in several cooperatively breeding species such as the Arabian babblers (*Turdoides squamiceps*), a bird species that I have been studying for over 30 years. Food transfer between adults of the same gender is almost without exception from a dominant to a subordinate (Kalishov 1996). It may occur several times a day throughout the year. The donor usually advertises the interaction with special vocalizations, and the receiver often emits begging calls. The food may be accepted submissively, accepted with impudence, or rejected. Interestingly, the donor is sometimes aggressive towards a subordinate that has rejected the food. Aggression occurs also in some of the rare cases in which a subordinate offers food to a dominant. These aggressive interactions are in line with Gurven's models of CS, because if donating food advertises the donor's claim for social status, then rejecting the offer reduces the status of the donor. They cannot be accounted for by the models of reciprocal altruism or kin selection (Zahavi & Zahavi 1997).

The use of costly signaling models to explain altruism was developed from my suggestion (Zahavi 1977) that altruism serves as a signal, and that the cost of the altruistic action is the investment (the handicap) that supports the reliability of the signal. The signal may advertise the donor's claim for prestige, or it may advertise the motivation of the signaler to cooperate. However, it can also function as a threat to potential rivals within the group. In a cooperative social system, a collaborator may at any time turn into a rival, seeking the right moment to replace the dominant. Advertising the quality of the donor may convince a subordinate to accept the dominance of the donor and not attempt to rebel.

Gurven considers the cost of food transfer by the direct value of the food transferred. I suggest that this is only a part of the cost. Food transfer in babblers, as well as among humans, is often done in times when food is abundant and its cost is trivial. An important part of the cost in food sharing is the consequence of the interaction itself. The donor displays its claim for social status (or social prestige, as I prefer to call it); the recipient is expected to accept and agree with this claim. If the receiver ignores the food, the social prestige of the donor is reduced (since there are usually other witnesses to such interactions). On the other hand, receiving lowers the social prestige of the receiver. There is a lot of variation in the way individual babblers accept or reject food donations under varying social circumstances, and in the way the donations are presented. Also, in babblers such interactions are as important among females as they are among males. Food sharing among humans may reveal similar meaningful variations in the details of the interactions and their cost in social prestige.

Social prestige is ever-present in social interactions. Like an invisible peacock's tail, it is important in attracting collaborators and deterring rivals.

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Nonmarket cooperation in the indigenous food economy of Taimyr, Arctic Russia: Evidence for control and benefit

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Abstract: Empirical data on food sharing in native Dolgan, Nganasan, and Nenets communities in Siberia provide evidence for hunter control over big game and fish, as well as likely benefits of inter-household sharing. Most food sharing occurs with kin and, thus, kin-selection-based nepotism cannot be ruled out. Reciprocal interhousehold sharing at meals occurs less often. Social context is discussed.

After describing four evolutionary hypotheses on hunter-gatherer food sharing, Gurven presents four key latent variables useful as indicators for evaluating nonmarket food transfer documented in ethnographic settings: depth, breadth, equality, and balance. Specific combinations of values for these variables as predictions for the explanatory models make the article a valuable contribution for those collecting field data on food sharing in the human-behavioral-ecology framework. Potential complications include: the specific combination of strategies characterizing food transfer based on given relationships in an ego's social network, the stage of food distribution, the type of resource being procured, the position in the life cycle, and local definitions of success.

Empirical research on food sharing among Dolgan and Nganasan in the Taimyr Autonomous Region in the Siberian Arctic shows the influence of a number of variables and models depending on the social context. For example, in the 1995-to-1996 period, 814 food-consumption events were observed in three types of locations in everyday settings. Of these meals, 546 cases included two or more native participants. In the regional capital, Dudinka, the majority of dyadic relationships at shared meals comprised mostly cognatic relatives, along with some friends. The majority of participants were female. In remote communities, including Ust'-Avam, Tukhard, and Kresty-Taimyrskii, cognatic dyads were less common but spouse and affine dyads had higher frequencies at shared meals. In most cases, affines represented a visiting household. During hunting trips, at reindeer herding camps, and at remote houses in the tundra, males who are close cognatic relatives and friends were the predominant participants at meals. The village and bush were the contexts under which more interhousehold food sharing occurred.

A thorough analysis of food sharing for five households in the Ust'-Avam area resulted in an interconnected network of 50 households. Seventeen households were considered to constitute the core because the elimination of one dyadic household link within this group would not isolate any of the other households. The remaining 33 households were peripheral actors, often connected through one link only. Focusing on household dyads, just over half were households related by kinship (44 of 84). Households related by cognatic kinship were associated with the majority (331) of interhousehold-meal observations (total 439) in Ust'-Avam and nearby bush. Following predictions from inclusive-fitness theory (Hamilton 1964) and generalized-reciprocity theory (Sahlins 1972), resource flow in this sample was most asymmetrical among pairs of households related by close kinship. This asymmetry includes household relationships exhibiting one-way flows of resources, especially from households with high producer-to-consumer ratios to households exhibiting lower consumer-to-producer ratios (i.e., young families). The context of much of this interhousehold sharing is one of children visiting and eating at their grandparents' or aunt's and uncle's house, providing further support for inclusive-fitness benefit.

Although non-kin also received meals in a one-way flow, such sharing relationships were less common – one household, consisting of an unrelated friend from outside the village, was hosted throughout her one-week visit; in another case, a young apprentice was hosted throughout a hunting expedition. Resource flow was more symmetrical, on average, between unrelated households, following expectations for reciprocal altruism and balanced reciprocity. Meals hosted between non-relatives show more balance. Meals hosted with kin show depth and bias towards relatives with children.

In a recent study, a number of independent variables were regressed on the interhousehold food-sharing network (Ziker, n.d.). The presence or absence of a kinship link between households was the most consistent predictor of interhousehold food sharing at meals. The physical proximity of households to one another is a marginal and weak explanatory variable, which drops out of significance when other variables are added. Because housing was assigned to families as it was built and became available in the 1970s through early 1990s in Taimyr villages, relatives were rarely assigned living quarters in close proximity. Kinship strongly influences food-sharing patterns independent of household location.

Reciprocal food-sharing relationships comprised 26 of the 84 household dyads (11 pairs of households in the core and 2 pairs of core-periphery households). When rank-order average household relatedness was compared to the rank of meals exchanged, the Pearson correlation (0.663) was significant ($p = 0.014$; two-tailed). Genealogical relatedness structures reciprocity, and the unrelated household dyads (3 of 13 pairs) received small total percentages of food shared at meals. The depth of sharing with relatives (and the asymmetry in the direction of young households) is highly evocative of kin selection-based nepotism.

Local social definitions of cultural success and proper behavior are also important for understanding food-sharing patterns among Dolgan and Nganasan. Hunters generally transfer the majority of procured meat and fish to their elders or spouses upon returning to the village, which implies a high degree of control over resources but a conversion to family property (Ziker 2002a). The elders or spouses (many of whom are the keepers of keys to storage areas) redistribute the raw food to their close relatives, especially those with children, as well as to friends and acquaintances in the form of either raw food or meals. Hunters and their families give to those people who ask for food (especially single mothers and pensioners), but they usually give relatively small portions of raw food and host such people at meals more rarely than relatives.

Although control is exerted at the kill and upon returning to the village, local understandings of property require hunters or their relative to share some portions of the catch with other people (otherwise "the hunt simply would not happen"). In cooperative hunts or fishing, the catch is usually divided equally among the participants. Signalling through food sharing likely factors into establishing long-term cooperative relationships with non-kin. Food sharing with kin may also carry a signalling function in terms of respect for elders and caring for relatives, who are supplied with food without asking. This is not to say that food sharing creates kin per se but that hypothetical signalling effects should not be limited to mating effort and long-term social-relationship building outside of kin. It is not clear that consistently generous individuals receive prestige, support, or social insurance beyond kin and close friends. Although claims of stinginess could carry a social cost reducing the benefit of hunter control, such communication is reserved for cases where the social relationship has already soured.

Author's Response

Tolerated reciprocity, reciprocal scrounging, and unrelated kin: Making sense of multiple models

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Abstract: Four models commonly employed in sharing analyses (reciprocal altruism [RA], tolerated scrounging [TS], costly signaling [CS], and kin selection [KS]) have common features which render rigorous testing of unique predictions difficult. Relaxed versions of these models are discussed in an attempt to understand how the underlying principles of delayed returns, avoiding costs, building reputation, and aiding biological kin interact in systems of sharing. Special attention is given to the interpretation of contingency measures that critically define some form of reciprocal altruism.

R1. Introduction

I would first like to thank all 13 of the commentators for their numerous insights and constructive criticism on the theory, methods, models, and evidence described in my paper. The enthusiasm displayed by researchers from anthropology, biology, and psychology attest to the widespread general interest in altruism and the particular interest in forager exchange. The commentators recognize that the particulars of food transfers in traditional, nonmarket economies have important implications for our understanding of human cooperation and how humans fit into the larger picture of cooperation in the animal kingdom. The commentaries acknowledge the difficulty of simultaneously generating unique hypotheses that can adeptly differentiate from among the four models – reciprocal altruism (RA), tolerated scrounging (TS), costly signaling (CS), and kin selection (KS) – and accurately representing each of these models in their myriad manifestations to avoid setting up any over-simplified straw men. It is especially true that TS, RA, and CS are macro-models, each containing numerous potential specifications. Major points from the 13 commentaries can be grouped into several broad categories: (1) questions about model choice, (2) bias in favor of RA over other models, (3) misrepresentation of TS, (4) controversy over interpretations of contingency measures, (5) phylogeny of sharing models, (6) sparse treatment of CS and KS, and (7) methodological issues.

R2. Model choice

Both **Getty** and **Sosis** ask why I did not consider mutualism as a separate category, rather than as a special case as I discuss it in the target article. I primarily discuss TS, RA, CS, and KS as important explanatory models of sharing among foragers and foraging horticulturalists. **Betzig** further argues that none of the models considers the possibility that conscripted boundaries may make alternative options to giving nonviable. More generally, alternative benefits of group living, including defense, mating, and social interaction, in addition to territory availability, may affect any calculus of giving.

Getty and **Sosis** make valid, relevant arguments, supported by additional comments by **Alvard**. However, I did not introduce mutualism until I discussed the interaction between production and consumption (sect. 8.2). The four models (TS, RA, CS, and KS) are mostly silent about how food is produced, and how production might influence sharing. While I consider mutualism a valid explanation of certain group production activities, such as Ifalukese fishing trips and Lamaleran whaling trips, defection is an unlikely scenario in these cases because each hunter chooses to hunt in their own self-interest (see sect. 8.2). Because there is no temptation to defect, some biologists do not even consider mutualism very interesting or worthy of the label of cooperation (see the discussion in Dugatkin 1997). First, although mutualisms may not be as problematic as Prisoner Dilemma-based cooperation, the coordination of individuals to achieve efficient outcomes, especially when multiple equilibria exist, is nontrivial (Alvard & Nolin 2002; Ochs 1995). Second, not only are per capita returns from engaging in these group activities high, but it may be *impossible* to forage alone or in groups below a threshold size, as Alvard reports.

As discussed in section 8.2, specific rules are fairly common for the purpose of guiding initial distributions of raw meat in these marine contexts. Thus, mutualism may explain special cases whereby substantial production requires groups of individuals. Even where foraging is possible in smaller task group sizes, mutualism may still explain why some individuals choose to forage in larger groups, when the return rate from being in a group of size n is greater than that of a group of size n-1, and, of course, greater than that from solitary foraging. However, in these cases, defection is still a theoretical possibility. After two men hunt capuchin monkeys, only one Ache may walk away carrying a monkey. The helper only contributes labor if he expects to receive a return from his effort, and the hunter shares his monkey meat at the end of the day as part of the tacit agreement. If a hunter does not sufficiently share the monkey with his helpers, then those helpers can hunt with other individuals who better adhere to the sharing norm. If defectors are punished, then social norms which promote cooperative mutualistic production may lead to substantial sharing. However, it is misleading to explain these outcomes as a result of only mutualism. As noted by **Smith**, payoff matrices are mutualistic only when a system of sharing and punishment norms makes them that way. Any invocation of mutualism is therefore not a satisfying explanation of group production and sharing.

I acknowledge in section 4.2 that the constraints of group living can affect the extent to which behaviors are individually advantageous. Limitations on living are most applicable in island populations, as **Betzig** reports, but whenever a home territory is better than an unfamiliar, distant territory, or when costs of transport and migration are substantial, we can expect to find people willing to make sacrifices when their only option is to leave the group. As suggested by Betzig, the application of skew theory (Hamilton 2000; Vehrencamp 1983) is useful for examining situations where individuals are manipulated, coerced, or harassed to the point where they are just slightly happier staying in the group than leaving. This logic has been applied by Boone (1992) in his treatment of elite competition and conflict

management between dominants and subordinates, and in the more general "harassment" model described by **Stevens & Cushman** (see sect. R4). I discussed Betzig's "no alternative" view as a last resort for when short-term costs of giving are not compensated by long-term gain, not because it's any less important or relevant than other arguments, but because testing this idea would require detailed information on the availability of other living options and the costs of leaving. These data are rarely available and difficult to obtain without experimental manipulation. It also requires that those who give more are the only ones being harassed or pressured to give, while the have-nots are the harassers, even though everyone in the group would probably benefit by not leaving. It is feasible that scroungers should endure stingy acquirers for the same reason that Betzig and Stevens & Cushman contend that acquirers should endure pesky scroungers.

Nonetheless, all else being equal, as discussed in the target article, greater mobility and nomadism should correspond with more options with respect to negotiations in the social environment. Most of the populations discussed in the target article are usually described as *egalitarian*, which implies individual autonomy and a general lack of anyone controlling the labor, wealth, resources, and decisions of others. These traits are idealized, but generally apply more to simple foragers than to complex foragers or intensive agriculturalists (Kelly 1995). With higher levels of sedentism, and greater benefits to group living unrelated to sharing, we should expect more compromised giving. As discussed in footnote 18, however, in larger, more sedentary villages with other attractions motivating the increased grouping, available evidence suggests patterns of more restrictive, contingent sharing.

Zahavi argues that KS and RA are unstable, indirect fitness models, and are therefore unlikely explanations for food transfers, both in Arabian babblers and in humans. Although I agree that giving to kin may not necessarily be KS, and contingency may not necessarily reflect RA (see sect. R5.1), I do not feel that either model should be discarded from this and future analyses. Both models are still useful for generating predictions about behavior. Parents feeding offspring may increase direct fitness, but whereas a direct-fitness argument suggests that giving to offspring should always be favored, a KS-based prediction would require benefits to offspring that are double the cost to the parent. When this condition is not met in a particular instance, parents should not provision their offspring. Similarly, although RA may be vulnerable to social parasites, the existence of contingency and norm enforcement (see sect. R4) can stabilize RA. The arguments that RA requires sophisticated cognitive machinery, or is difficult to maintain, and therefore unlikely to be common in the animal kingdom, have existed ever since Trivers first proposed RA as one solution to non-kin-based cooperation. If humans meet the rigid conditions required for RA, then it does not matter that many other species do not display RA because they do not meet the same conditions. Stephens et al. (2002) reports that animal discounting rates are much higher than reported human discount rates, and this alone may account for some of the differences between human and nonhuman tendencies towards RA. Nevertheless, as I argue in the paper, the version of a Tit-for-Tat-based RA, as typically modeled in mathematical treatments, is probably unlikely even among human foragers.

R3. RA Bias

Animal researchers have the onerous task of demonstrating that the species they study display the more cognitively demanding RA in a natural environment, where the default is something more akin to TS when among non-kin. Anthropologists, however, have historically taken RA (or "generalized reciprocity") as the assumed human forager pattern, whereas other explanations such as TS required more substantial argument to convince anthropological audiences. However, quantitative data necessary to assess the extent of RA have been collected only in several groups. Some recent development in behavioral ecology has reversed traditional thinking such that TS or CS is responsible for sharing (Hawkes 1990; 1992; Hawkes et al. 2001), men's foraging decisions (Bird 1999; Hawkes 1993), and nuclear family formation (Hawkes et al. 2001), with implications on human life history via the "grandmother hypothesis" (Blurton Jones et al. 2001; Hawkes et al. 2002). To some extent, the almost exclusive focus on hunting and the sharing of large game has produced a biased perspective on forager exchange. To be fair, even if TS and CS explain the sharing and production of big game among the Hadza, and turtles among the Meriam, such arguments alone are insufficient to make generalizations about foraging economies and nuclear-family formation. My comments regarding the sharing of small game, and non-meat items were not made to mislead the reader, as **Smith** suggests, but to direct attention to important questions necessary for more general inference about the sexual division of labor, the theory and evidence underlying such a division, and to help guide future empirical analyses of sharing. For these reasons, one of my principal goals for the paper was to place RA back on the proverbial dinner plate, after its premature abandonment by behavioral ecologists in recent years. To this end, I have purposefully focused energy in this paper towards discussion of the components of RA, bargaining, and the evidence in favor or against RA.

R4. Relaxed versions of TS

I did not intend to focus attention on RA at the expense of misrepresenting TS or any of the other models. First, I may have been unclear in my discussion of "producer control" over distributions. I agree with **Franzen** that control is neither completely absent nor completely present. TS does not require an absence of control, inasmuch as hoarding may be prohibitively costly, and so individuals may give up some control when the defense (or other) costs are too high. Control is best viewed as an outcome that can vary over time, across individuals and resources, rather than as an automatic property of a resource. My point in demonstrating that individuals often keep way more than $1/n$ in their families for a variety of resource types, and other evidence of significant bias in distributions, is that producer control is hardly uncommon among foragers and forager-horticulturalists. Defense or exclusion costs have never been measured in any population, yet anecdotes of demand sharing suggest their existence. However, the abundant evidence for control implies that defense or exclusion costs are not so high, which suggests that conditions do not favor TS.

Smith, **Sosis**, and **Stevens & Cushman** all question whether control even matters in more generalized versions of TS. As I mention in Note 10 (perhaps better suited in the

body of the target article) referring to prior modeling by Vickery et al. (1991), and as reiterated by **Smith** and **Franzen**, some level of scrounging is likely to be tolerated in a population. I do not deny this. Thus, **Alvard** notes that graduated income taxes may exist among some foragers, and even if good producers pay proportionally higher taxes due to increased pressure or harassment by scroungers, the net consumption payoffs to being a good producer may still be sufficiently high. Stevens and Stephens (2002) present a harassment or sharing-under-pressure model, where beggars harass acquirers and thereby affect the net consumption payoffs of the acquirer. As in Blurton Jones' tolerated theft model, manipulation by hungry or needy individuals produces a mutualism whereby beggars gain food, and acquirers avoid costs. The cost of harassment is a reduction in feeding efficiency, or more generally, as **Brown** notes, attracting the attention of other group members. When there is substantial producer control, their model requires that harassing beggars receive benefits by collecting food scraps or by stealing. These conditions make widespread harassment unlikely among human foragers. First, stealing and scrap collecting are not very common among adults and are sometimes met with punishment or ostracism. When left unpunished, the few individuals known to scrounge are usually regarded as low status (see sect. 4.4). Although harassment may not affect feeding efficiency, it may affect reputation. Thus, again we are confronted with the scenario that people give to avoid being called stingy, and being called stingy may matter most when people have high degrees of interdependence in production and/or reproduction.

How else might TS be more "subtle and pervasive" than I have described? As mentioned in the target article, egalitarian sharing is expected when power, marginal costs of scrounging and information gain, and utility or value for additional food are similar across potential recipients. Again, although none of these have been measured in field settings, these joint conditions are unlikely to be met. Without specific models of optimal sharing breadth and depth, it is difficult to argue whether 9 family recipients out of a potential 15, for example, is indicative of TS, or of RA. Among sedentary Ache living at a horticultural reservation, an analysis of sharing breadth of meat brought back from temporary foraging treks indicated that breadth was still far below what one would predict, even after knowing the number of meat items present on the reservation at any point in time (Gurven et al. 2002). When asked about who the recipients will be prior to a distribution, I found that Ache acquirers knew both the number and identity of who the actual recipients would be (Gurven et al. 2001). They did, however, usually underestimate by about one recipient on average per distribution.

Finally, although the existence of cultural sharing norms sometimes results in a pattern where food distributors and acquirers are separate individuals (see sect. 4.1), the existence of this pattern does not mean that sharing decisions cannot be modeled as if they were not (**Sosis**). I agree with Sosis that none of the models can explain why different cultural norms evolve, or how precisely they are maintained. Nonetheless, we should expect cultural rules governing distributions to at least partially reflect the interests of the acquirer, so as to motivate future production. Otherwise, individuals produce food only because of threats or harassment by other coercive individuals. When non-acquirers distribute food, some leverage over strategic giving on the part of the acquirer may be lost, but the net benefits to the acquirer may still accrue according to the logic of KS, CS, RA, or TS. Thus, while the specific character of many sharing rules is culturally variable, most rules direct shares toward the family of the acquirer, kin, in-laws, task group members, capital owners, respected elders, and fertile females. Modeling decisions as if they were directed and controlled is often done in behavioral ecology because it provides an easy framework for devising and testing null hypotheses about behavior, and for examining deviations from expectations. For example, marriage decisions of women have been modeled according to the potential fitness payoffs of different arrangements, even though female choice may be compromised by the desires of other decision makers (Borgerhoff Mulder 1990).

The expression of specific norms in different cultures may be intricately linked to the incentive structure that binds production and distribution (sect. 8.2). Current models of cultural transmission do not address these important links. The potential gains to cooperation in economic and social activities will vary among groups, subgroups, and ecologies. For example, a widespread sharing rule that does not bias food towards kin over non-kin, as among the Ache, may be expected when efficient task and residential group size includes both kin and non-kin. Among the Lamalera, boat owners may receive larger shares because they provide capital that is crucial to group production. If hunting equipment is difficult to manufacture, then tool makers may receive portions of kills. Norms also vary cross-culturally with respect to the tolerance for begging, harassment, and scrounging behavior. Under what conditions does demand sharing become a culturally acceptable set of behaviors? Sharing breadth and depth are very high among both the Hadza and the Ache, but their different behavior when playing several economics games designed to measure altruism and punishment, suggests that norms regarding these aspects of cooperation may indeed vary. Any explanation that relies on cultural variability in norms needs to explain why these norms differ in the first place.

R5. Contingency

R5.1. Reciprocal TS

The distinguishing feature of RA is a demonstration of contingency. As **Brown** points out, it is important to show that contingency is not due to other intervening factors. Two ways that contingency can occur without strict RA are when individuals simply bias resources towards kin or neighbors. For this reason, I showed in my work among the Hiwi and Ache that contingency still existed even after controlling for average or closest kinship relation between members of giving and receiving families, and for geographical proximity between families (Gurven et al. 2001; 2002). Nonetheless, **Brown** and **Stevens & Cushman** reiterate the point I made that a significant contingency correlation can reflect a form of TS where individuals frequently switch the roles of producer and recipient. This is reciprocal TS. First, if the TS manifests itself as neighbors receiving more food than other band members, then controlling for physical proximity should help distinguish between reciprocal TS, versus RA. Second, foragers often consume resources back in camp, where the presence of others makes distribution very

likely. A pattern of reciprocal TS should show a greater tendency towards consumption at acquisition sites. Third, a pattern of reciprocal TS switches the focus of contingency away from sharing and towards production based on turn taking. With reciprocal TS, contingency should focus on work effort rather than amounts given and received. I make the argument in section 8.3 that this form of contingency may be most prevalent in small-scale, highly egalitarian interdependent groups, where sharing appears to otherwise be unconditional. Without contingency focused on work effort when subsequent sharing is TS, there will be little incentive to produce, and scroungers will thrive (Blurton Jones 1987). Thus, any significant contingency measures based on quantities or amounts may be spurious, and may not reflect the actual psychological or cognitive processes of fairness assessment and cheater detection.

R5.2. How to measure contingency?

The measurement of contingency is still at an early stage in terms of current research design, parameterization, and statistical methods. Quantitative sharing studies have typically spanned anywhere from two months to a year, and individuals, households, focal resources, or consumption events are usually sampled randomly (or sometimes nonrandomly) within that time frame. First, even though contingency refers to returns made after a time delay after giving occurs, measures of contingency primarily correlate the total amounts transferred across pairs of families over the total sample period. Contingency is measured this way because any single time boundary meant to separate shares given and those received would be arbitrary and may differ across specific pairs of families. Given limited samples, estimates of amounts or percentages exchanged among any specific pair of families may be too few, or too biased due to sample error. Nonetheless, if the time horizon of returning resources falls within the time span of a study, and people are adequately and representatively sampled, then correlations between giving and receiving over the sample period should correlate strongly with "true" contingency. Second, the currency of kilograms, calories, or standardized versions of these amounts in the form of percentages, may not correspond to the value each food receipt provides to a recipient family.

Preliminary work exploring alternative measures of contingency that more accurately reflect value, rather than amount, shows mixed support for the notion that value-based contingency is stronger than quantity-based contingency. I estimated total value family *A* transferred to family *B* by summing the logarithms of each individual quantity *A* gave to *B*. Although this method does not incorporate the value of trading different types of resources, it emphasizes the diminishing returns in value associated with the transfer of larger shares. Among the Ache, value-based correlations for transfers of all foods, forest items, and cultigens were stronger than quantity-based correlations. The value-based correlations were over twice as large as the quantity-based ones. Among the Hiwi, there was a slight reduction in contingency when using value rather than quantity for meat and all foods, but a larger correlation when examining transfers of fish. As suggested by **Franzen**, contingency based on the frequency of transfers may give more insight into potential value, rather than my measure of value based on the logarithmic function. Frequency-based contingency was about three times greater than quantity-based contingency among the Ache, but no different among the Hiwi (Gurven, in press).

Even though value-based contingencies may be stronger on average than quantity-based estimates, there is still no guarantee according to RA that exchange will be balanced in terms of value. As implied in the treatment on bargaining (sect. 4.3), the amount of production exchanged among pairs of individuals is subject to negotiation, and RA-based exchange is expected whenever the long-term benefits outweigh the short-term costs. Equal exchange is predicted only when the bargaining chips of pair-wise interactants are equal. However, relative bargaining power has been examined in only two groups, the Ifaluk (Sosis 1998) and the Hiwi (Gurven et al. 2000b).

Despite the problems with empirical estimates of contingency, additional lines of evidence lend support to the notion that some form of calculated contingency exists among social actors. Slacking by specific others in many foraging bands hardly goes unnoticed, and, as discussed in section 4.4, extreme examples are often treated with some form of direct or indirect punishment. Performance in cheater-detection experiments is consistent with a psychology that can readily detect cheaters in social contracts, even if not tracking detailed scorekeeping (Cosmides 1989; Sugiyama et al. 2002). Many Ultimatum Game economics experiments have shown that people punish stingy individuals at personal cost in a variety of contexts. In multistage Trust Games, subjects reward those who were previously more generous to them, even though such rewards are costly. In fact, an increasing number of economics experiments reveal that people are highly cooperative and policing, even when games are one-shots without opportunities for reputation building or reciprocity (Fehr & Fischbacher 2003). Thus, a more generalized version of a contingent psychology is based on "strong reciprocity." In strong reciprocity, norm-abiding cooperators are rewarded and norm-violating shirkers are punished, even when it is not in the strong reciprocator's long-term interest (Fehr et al. 2002; Gintis 2000). That violators of cooperative norms are frequently punished in economics games under conditions disfavoring RA or CS suggests that human social psychology provides a baseline for effective pairwise and group-oriented reciprocation strategies. However, as **Smith** correctly points out, norm enforcement and strong reciprocity introduce a second-order collective action problem. Cultural group selection, a system of differential costs or benefits to enforcement, or costly signaling, are possible solutions to this problem.

R6. Phylogeny, history, and RA

Both **Brown** and **Stevens & Cushman** favor a less restrictive TS explanation for sharing among humans because it is more parsimonious, does not require high levels of cognition, and may be the best explanation for sharing in nonhuman primates (cf. de Waal 1989; 1997b; Mitani & Watts 2001). Although these features suggest that RA is unlikely to occur in the animal kingdom and presumably among humans as well, they do not constitute evidence against RA in human populations. Just because male parental care is rare among most mammals, and the conditions favoring it are restrictive among many social animals, does not mean we

do not find abundant examples of male provisioning and direct care of offspring among humans. RA and widespread sharing are unlikely candidates as strong explanations of sharing among primate species subsisting on plants, fruits, and insects. The human foraging niche, which depends on difficult-to-acquire, nutrient-dense resources, is critically linked to widespread sharing (Kaplan & Gurven, in press; Kaplan et al. 2000). These hunted and extracted resources often arrive intermittently in large packages, and their acquisition requires a substantial period of learning.

Among groups such as the Ache, Machiguenga, and Piro, food production does not exceed consumption until the late teens, and thus a large portion of the early life span is subsidized by other group members. The relatively high fertility of humans compared with chimpanzees, especially with multiple dependent young, means that parents in their years of peak production often cannot fully provide sufficient calories for their offspring. Sharing among families is therefore necessary and often widespread. Presumably sufficient selection pressures have shaped the form and character of sharing common among foragers, such that relatively novel forms of cooperation, including RA or strong reciprocity, could have evolved. Furthermore, the analytical result that RA is unstable in large groups only suggests that individuals are unlikely to interact in unstructured groups. The available evidence on humans living in larger groups in small-scale, traditional contexts (e.g., Hiwi, Ache at the reservation, Tsimane), confirms that people do not generally share with everyone in the group, but instead share with a subset of families in the residential group. Thus, one is not required to remember a precise scorekeeping history of ego's interaction with every other individual in the group. Language also enables humans to surmount prohibitively high monitoring costs because frequent gossip can provide up-to-date information (albeit of questionable reliability) about other group members.

Moore offers one plausible scenario for the evolutionary history of human food sharing based on KS precursors, followed by TS, then CS, and finally RA. Moore is correct when he cites my failure to address the evolutionary history of these four models, via detailed reports of nonhuman primate sharing and inferences about prehistoric sharing practices. Whether the four models evolved independently or sequentially is an important question, but, in either case, it is still possible to view these models as "contingent aspects of an evolutionarily integrated behavioral package." As I discuss in section 7, transfers should occur when the sum of all expected benefits to giving (e.g., inclusive fitness and future returns of meat, sex, or support) outweigh the immediate loss of value associated with complete consumption, and any other defense costs associated with hoarding. As opportunities change over time affecting short-term and long-term costs and benefits, the relative strength of each model in explaining any particular or set of sharing episodes will vary. Several examples illustrate this concept. All else being equal, as fertility of close kin increases, so may the relative benefits of nepotism. If people visit from a different territory that is usually productive when the home territory is not, giving to them now may yield benefits in the future in terms of reciprocal access to their territory and foods. If several of those visitors are fecund women, males may be motivated to engage in costly sharing displays. If important social partners temporarily or permanently leave the village, their previous partners may initiate targeted costly displays to attract new social partners.

R7. What about CS?

Both **Zahavi** and **Smith** suggest that I underestimate CS. Dominant Arabian babblers persistently transfer food to subordinates, and rejections of food offerings are met with aggression. The interpretation of these patterns is that food transfers "advertise the donor's claim for social status," consistent with CS. Zahavi argues that these patterns are inconsistent with RA. However, a characteristic of RA is that it creates indebtedness on the part of the receiver. If excess food forced upon subordinates indebts those subordinates to reciprocate, even if at lower levels, such giving might still be consistent with RA. Having others in your debt is consistent with RA, even if it also raises your status relative to others. Tit-for-tat RA is an unlikely expectation, whereas a social insurance proposition described in section 5 is more likely. The debt created by RA is commonly described in forager ethnographies, where generous offerings are sometimes met with suspicion. This pattern is mentioned by **Lefebvre** in German and Russian cultures, and there is experimental evidence in the form of rejection of large offers in the ultimatum game by the Au and Gnau in Papua New Guinea (Tracer 2003). The coerced giving observed among Arabian babblers is not analogous to giving among human foragers. Among foragers, demand sharing and giving in general is often described as a cultural leveling mechanism, meant to *reduce* dominance, status, or prestige differentials, rather than promote them. Also, dominant individuals, including among chimpanzees and other nonhuman primates (**Brown**), as well as among the Ifaluk (**Betzig**, **Sosis**), usually receive more rather than less food, and from more distributions.

Most tests of CS among humans have predicted a large breadth of recipients during distributions, because a wide audience aids in broadcasting the signal of giving. As **Smith** remarks, the large audience is not a requirement of CS, even if that has been one of its most straightforward predictions with respect to sharing. Ultimately, the existence of language as a broadcast tool means that any breadth is equally consistent with CS. However, of course gossip or other indirect informational exchange is cheap and may be unreliable. To the extent that reputations emerge through gossip and social networks, language cannot be ignored as an important means of signal broadcast and signal manipulation. Much experimental evidence suggests that communication, despite its cheapness and lack of enforcement, is often reliable and effective for enacting coordination (Ledyard 1995). If transfers are directed at specific few people, Smith argues that this kind of giving still may have a strong CS component. It is important to distinguish that this form of CS of donor intent is different from CS of phenotypic quality. Signaling intent is expected precisely when payoffs to cooperative partnerships are high, when costs of defection are high for the cooperator, when sufficient variation exists among potential partners, or when there is uncertainty about partner quality and intent. In fact, much of the difficulty in maintaining RA in populations is due to the frequent null assumptions of random mixing of strategies or individuals, which destabilizes cooperation. Selective partnership or restricted cooperation when in large groups can

maintain RA (Boyd 1991). Thus, CS may be important as a means of attracting, testing, and maintaining cooperative partners within the context of RA. This is one example where two models, CS and RA, may be nested. KS has also been described as a potential primer for RA (Axelrod & Hamilton 1981).

R8. Problems with kinship

Getty feels that I prematurely abandoned KS as an explanation for sharing patterns and asks what a "null model" of sharing without kin bias might look like. The requirements of Hamilton's rule may not be so difficult to achieve, and so when the benefits to a recipient, devalued by the genetic kinship between the donor and receiver, outweigh the costs to the donor, conditions for kin selection are met. I argued that physical proximity can confound this relationship, and that the empirical result that proximity is a stronger predictor of receipt than kinship among the Hiwi raises the possibility that kinship may be overemphasized in sociobiological treatments, and, based on subsequent work among the Ache, that close kin may make better RA partners than do non-kin. In no way did I wish to discard nepotism, but rather, I intended to nest nepotism within a larger framework. Others have taken a similar stance. For example, Wilson and Dugatkin (1991) argued that reciprocating strategies such as Tit-for-Tat can evolve among close kin and can replace strategies that always act kindly towards genetic relatives. The reason why I did not spend very much attention on kinship was because most of the controversy within behavioral ecology focuses on CS, TS, and RA. However, there are several important aspects of kinship that require further attention.

First, **Hames** correctly identified an important "targeting" problem associated with kinship. At a general level, individual *A* wants individual *B* to consume a share of resource *X*. The targeting problem manifests itself in two ways. First, an acquirer may not feasibly be able to direct shares to a specific other person. The greater the number of indirect links between *A* and *B*, the decreased likelihood that *A*'s desires will be realized. When *B* receives less resource than *A* intended for *B*, *B* also may lose additional opportunities for gain via subsequent sharing of the resource. An intention to send 2 kg of fruits to *A*'s nephew might require *A* to send 3 kg. Second, kin may not use a resource in the same way as the acquirer intended. For example, distant kin member *F* might receive fewer tubers than close kin *G*, but *F* trades several of his tubers for a portion of duiker meat while *G* consumes her total share, such that the net benefits *F* and *G* receive are identical. In this case, when conflicts over resource use are evident, less food might be given to a specific kin member. Additionally, small children and other individuals are often asked to deliver food portions to members of their families or to members of other families who may live nearby. In no study have acquirers ever been asked who would receive shares in secondary distributions of resources given out during a primary distribution. Nor has any study explicitly examined the extent to which *A* initiates and directly gives food to *B*, whether food is given via intermediaries, or given only upon request (either directly or indirectly). Sharing analyses that measure consumption or eating "hits" (e.g., the Yanomamo, and the Ache on forest treks) do not examine the intermediary links between original acquirer and recipient. However, Ache reservation and unpublished Tsimane food-transfer data examine the identities of individual acquirers, donors, recipients, and consumers. Among both Ache on the reservation and among the Hiwi, two-thirds of all food was given away in primary distributions, and roughly half of primary shares were redistributed to other families.

In analyses of pair-wise exchanges among Ache and Hiwi, I focused mainly on exchange at the level of the nuclear family because of the targeting problem, and the observation of frequent indirect giving. Kinship between families *A* and *B* was operationalized as the closest genetic relationship between any member of *A* and *B* in my prior publications. Kinship between families can also be defined as the average relatedness between all members of *A* and *B*. The correlation between these two measures for the Ache was 0.88 ($p < 0.0001$), and no empirical results changed significantly when using one versus the other of these two measures. A project is currently under way to explore bias in food transfers towards consanguineal versus affinal kin, as an attempt to infer how conflicts in individual interest result in family-level decision making.

Another important issue concerning kinship focuses on its embeddedness within any population. As **Ziker** points out, kinship structures social relations. It may affect where people live, with whom they engage in productive activities, and the frequency and intensity of social interaction. Wiessner (2002) argues that the Ju/'hoansi choose to live in camp with close kin, with distant kin and unrelated individuals living in other camps, and thus campwide sharing favors high levels of nepotism. Good hunters also have more close kin living in camp, and for longer periods of time. Thus, even if !Kung sharing were TS (which it does not appear to be; Wiessner 2002), control over the choice of recipients is still possible. In another example, while there was no kin bias in sharing distributions during forest treks, I found a strong kin bias in giving between families among the Ache at the reservation, even after controlling for proximity. One reason for the lack of bias during foraging treks is because people do not selectively leave the reservation to forage preferentially with close kin (Gurven et al., in press). To argue that kinship is unimportant among the Ache would therefore be misleading.

Kinship, in combination with marriage rules, links people together in intricate ways, especially in small bands, such that calculated contingency may not be as important when there are many coincident interests. When individuals choose to live nearby to close kin and other individuals with whom they wish to share, proximity may be a better predictor of sharing than is kinship. However, in contexts where groups are large, kinship relations are diffuse, or individuals vary in their partner quality, the net benefits of nepotism may be outweighed by potential benefits of CS or RA. **Ziker**'s experience with the Dolgan and the Nganasan suggests that, despite living in large villages, most sharing occurs with close kin, and that this sharing is not symmetrical. This sharing with kin is therefore unlikely to be RA, and must be KS or TS.

According to **Ziker**, RA occurs mostly with unrelated households. As an interesting contrast with other studies, Ziker finds that kinship is a more significant predictor of inter-household sharing than is proximity. This is probably due to the fact that, in Taimyr, people did not have any choice over residence location because "housing was as-

signed to families as it was built" and "relatives rarely were assigned living quarters in close proximity." However, the extent to which kin-based sharing also meets the conditions for RA can vary. Like the Dolgan and the Nganasan, Ache at the reservation preferentially share with kin, but a major difference is that giving and receiving is much more symmetrical among close kin than among distant kin and unrelated families. The opposite result was found among the Hiwi. We therefore find in several populations evidence for both RA and KS, but they differ in the extent to which close kin identify as reciprocal sharing partners. Several of the issues concerning kinship just briefly mentioned here will be addressed at greater length in a subsequent publication (Allen-Arave et al., in preparation).

R9. Methodological concerns

Getty questions my use of path analysis as an analytical tool for teasing apart predictions from the four evolutionary models of sharing. I agree with his assessment that there are numerous ways to specify a path model, many of which may be statistically significant. The path model discussed in the text is not necessarily the best model that fits the data. I chose the particular specifications based on the proposed theoretical relationships between variables. Even with my specification, however, I would not conclude that "relatedness is only two-thirds as important as distance in determining giving" (Getty's commentary, para. 7). In estimating the overall effect of relatedness on giving, one needs to sum up all direct and indirect routes. The overall effect of relatedness on giving among the Hiwi, using the path estimates given in Figure 3, is 0.191, which is greater than the overall effect of distance on giving, 0.172. Only 47% of the overall effect of kinship on giving is through intervening variables, whereas only 15% of the distance effect is intermediated through other factors. My main point with the exercise of using path analysis to explore Hiwi and Ache sharing was that multivariate models are indispensable when testing hypotheses from several models which all use many of the same variables. Path analysis, or, more generally, structural equation modeling, is but one approach. Multiple regression analysis is another. The advantage of path analysis is that it depicts the causal relationships between variables in a meaningful way. Not all specifications are possible or even desirable. For example, kinship and proximity should not be switched, because while kinship can influence who your neighbors will be, proximity cannot determine kinship. The path model specification I chose allowed tests of multiple hypotheses from several explanatory models in a single procedure, and did not favor one model over another. If it is believed that an alternative path model specification would lead to different conclusions, then alternative specifications can be easily tested. Path analysis also more directly incorporates the collinearity between "independent" variables. If all variables are truly independent, then multiple regression is a sufficient approach.

Hames draws attention to the way I operationalized family "need" as the number of consumers in a family. Elsewhere, I have used consumer-producer ratio with no significant changes in results, presumably because the two measures were highly correlated. The Yanomamo case which carefully examined sharing with respect to need (Hames 2000) is an illustrative one that I referenced but unfortunately did not give enough attention to. It is important because it shows that even in a fairly egalitarian social environment, where begging and harassment for food are common (Hames 1990), giving is biased more towards those who give back, rather than towards families who possess greater need. Of course, "need" defined by the consumer-producer ratio of a family, though a more sensitive measure than the number of consumers, is still just an approximation of relative demand and does not reflect actual production and consumption of family members.

R10. Additional concerns

Although many models of sharing are agent centered, few explicitly incorporate intention and social expectations. **Lefebvre** describes an interesting model based on the "reflexive intentional model of the subject," or RIMS, whereby transfer outcomes are modeled as a function of intention, social pressure, and utility. The model identifies individuals who favor positive gains from prestige, and those who favor positive gains from consumption. Although the components of the model are useful and represent key aspects concerning sharing decisions, the model itself is not evolutionary. It is also unclear how explanatory the model as stated can be, because there are no a priori justifications for ascribing values of x_1 (social pressure), x_2 (subjective evaluation of normative pressure), and x_3 (intended share). I like Lefebvre's explicit inclusion of the conflict between individual intention and limitations on realizing that intended outcome via social pressure. However, what are the costs of violating social norms or pressure? Without any means of weighing costs of norm violation against the benefits to hoarding (whether status seeking or consumption seeking are primary goals), we have not moved any closer to understanding individual variation. There is also no indication why certain individuals should value consumption while others value social status (such as age, sex, family dependency, etc.), and the lack of any frequency dependency does not shed any insight into the relationships between production, consumption, and distribution.

R11. Conclusion

I agree with **Hames** that prior to any comprehensive testing of competing sharing models, one should consider the adaptive problem of sharing in the first place. I state this in section 1 of the target article: "A complete behavioral ecology of food transfers should explain the function or purpose for food transfers in the first place, as well as the social mechanisms responsible for maintaining different levels of food transfers within populations" (para. 8). The two adaptive functions primarily discussed in the article are risk, or variance reduction, and costly display of phenotypic quality and intent. Others include increased efficiency from turn-taking or specialization through trade, and the formation of coordinated, cooperative endeavors based on mutualism. Food transfers can serve multiple functions simultaneously, and the plethora of models explaining transfer patterns suggests that many causal pathways will lead to the outcome of sharing.

The reports of extreme widespread, unconditional sharing among groups such as the Hadza and the Ache (during forest treks), if true, may not be very representative of for-

agers, either in the present or in the distant past. The cases for TS and unbalanced RA are strongest when resources are highly unpredictable. There is increasing evidence that small game and other significant, but less risky, protein and lipid sources may have been important features of early human diets (Stiner et al. 2000). Even among the Hadza, who are known for their big-game hunting practices, small game, honey, and other food sources besides large game contribute significant calories to the diet (F. Marlowe, personal communication). While significant contingency estimates in small groups may be consistent with reciprocal TS combined with punishment and with RA, a focus on important ecological changes can provide much insight into the contingency of contingent exchange. The variation witnessed by groups undergoing transition, by seasonal variation in diet and opportunities, by increased trade with neighboring populations and increased interactions with the market economy, and by increases in group size and privacy, are all associated with shifts in the sharing economy towards greater pairwise contingency. For example, in ethnographic cases of modernizing foragers in transition, alternative food resource options are often eagerly taken which allow foragers to reduce risk of daily food shortfalls by means other than widespread daily sharing (Cashdan 1980). Even though game supply has decreased over the past 20 years, and demands for food have increased among the Dobe Ju/'hoansi, sharing of large game is more restricted now than it was 20 years ago, mostly confined to close kin within a single camp, with the remainder sold to pastoralists or government workers (Wiessner 2002).

If human social psychology is constrained within certain boundaries with respect to fairness and punitive sentiment, as a result of a selective history of KS, TS, CS, and RA over evolutionary time, then variation in behavior is a function of personal predilections interacting with the culturally variable formal and informal institutions that create incentives to behave in specific directions. Human behavioral ecology has been useful for explaining intra-group variation in food sharing as a function of resource ecology, group size, sex, and age. Future interdisciplinary research should link general functional explanations of sharing that focus on ecology, individual fitness benefits, and the dynamic interplay between production and distribution, with cultural transmission models of group-specific norms, and proximate psychological models that describe emotional and cognitive intent.

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Letters "a" and "r" appearing before authors' initials refer to target article and response respectively.

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