avenue out of the debate may be to model food transfers as a signaling 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 2004).

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 rewards. 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.