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

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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 & Bird 2000).

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: Food sharing among cooperative fishers

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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

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