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 western 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.

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

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

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:

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

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:

$$x_3 = 1/(1 + \text{SQRT}[1 - x*]) \qquad (3)$$

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:

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

Two roots out of the three belong to interval $[0,1]$: $x_3^{(1)} = 1$ and $x_3^{(2)} = (\text{SQRT}(5) - 1)/2 = 0.618. \ldots$ 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:

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

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 (1963) 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).

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