

Food-Sharing Models

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Food sharing has been a topic of long-standing interest in anthropology and other social and biological sciences, being tied to notions of fairness, generosity, reciprocity, and egalitarianism. Food sharing is one of the most obvious and essential forms of cooperation among hunter-gatherers and is intricately linked to the evolved human life history and foraging niche (Jaeggi and Gurven 2013a). Unlike other apes, human children are provisioned for almost two decades, and even young families with multiple dependents require caloric subsidies from older generations; investing in the learning of skill-intensive foraging skills early in life by necessity leads to severe underproduction early in life but is followed by massive surplus production later in life. Furthermore, the targeting of high-yield but high-variance resources such as big game is made possible only by the pooling of production among multiple foragers.

Other primates share food too. Infants of various species are allowed to take food from their mothers or other caretakers for nutritional or informational benefit, and sharing among adults of some species (such as chimpanzees), reluctant as it might be, tends to map onto enduring social relationships based on kinship and reciprocity (Jaeggi and Gurven 2013a). Yet, at some point, hominins started to specialize in the production of large, high-value food items that provided the energy necessary to fuel the evolution of large brains and required substantial cooperation among mates and group members (which in turn may have increased selection for larger brains).

Not surprisingly, then, a significant and growing body of research by evolutionary anthropologists has focused on food sharing in human foragers as well as nonhuman primates (Gurven 2004; Jaeggi and Gurven 2013a). This entry summarizes basic theoretical models and general empirical findings of this research; for a more detailed review of recent empirical results and future research challenges, see Gurven and Jaeggi (2015).

Why share food? Theoretical models

All organisms have been selected to maximize access to fitness-relevant resources at minimal cost, but this raises the question of why they then give up food that has taken time and energy to acquire. Theoretical models of food sharing (Table 1) go back to the origins of evolutionary game theory, developed for animal contests in the 1970s. When two individuals encounter a resource, they can either be willing to fight and risk injury (“Hawk” strategy) or merely display in the hope of outlasting their opponent but refrain from escalated fights (“Dove” strategy). When such contests are asymmetric (e.g., when one individual is stronger or one would derive greater value from the resource), a mixed Hawk/Dove strategy will do best: play Hawk when you are stronger or you value the

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Table 1 List of theoretical models explaining food production and food sharing, with their empirical support.

<i>Model</i>	<i>Summary</i>		<i>Requires</i>	<i>Empirical Support</i>
Tolerated scrounging	Cost (owner) < Benefit (recipient)		Owners value resource less than nonowners	Sharing most common for large items: yes Sharing random or only predicted by resource-holding potential: no Sharing often predicted by kinship: yes
Kin selection	Cost (owner) < Benefit (recipient) × Relatedness (owner–recipient)		Control over distribution, kin recognition	Food production aimed at maximizing inclusive fitness benefits: yes
Reciprocity	Cost (owner now) < Benefit (owner later) × p (reciprocation)		Control over distribution, assortment of reciprocators	Sharing predicted by receiving: yes Production of shareable food predicted by presence of allies or mates: mixed
Costly signaling	Food production reveals quality; sharing broadcasts this signal		Signaled quality useful for partner choice	Good hunters have greater fitness: yes Food production aimed at maximizing signaling benefits: mixed

resource more, otherwise play Dove (i.e., defer to Hawks). This is how contests over resources are often settled in nature, avoiding unnecessary escalation.

It follows that we should not observe sharing of resources when differences in fighting ability, or “resource-holding potential,” are large, because strong (dominant) individuals playing Hawk will gain preferential access to resources, and weak (subordinate) ones playing Dove will often not. But, given similar resource-holding potential, it is important to assess who should place greater value on the resource and therefore play Hawk. There are two possibilities. First, the initial finder of the resource (the “owner”) places greater subjective value on the resource and plays Hawk, while latecomers play Dove. This outcome is reflected in the well-described endowment effect in humans, wherein people overvalue objects in their possession. It is also consistent with “respect for ownership,” as famously described by Hans Kummer, for male hamadryas baboons competing over the same female (Kummer, Götz, and Angst 1973). The second possibility is the reverse: latecomers value the resource more and play Hawk, while owners play Dove. In this case, the resource will be shared—that is, (some of) it will pass from owner to nonowner.

In terms of how these game-theoretical models relate to food sharing in humans and other primates, Nicholas Blurton Jones (1987) used the logic of the asymmetric Hawk–Dove game to argue that sharing, as opposed to respect for ownership, will be common when resources are large and rare. If resources are large, owners experience diminishing returns to consumption such that the next piece of food will have a lower value to the owner than the one just eaten (see Figure 1). Hungry latecomers, however, place greater value on these same food pieces, especially if the resource is rare and they are therefore unlikely to have found food themselves. Owners of large, rare resources, as often pursued by human foragers, should therefore be selected to share (play Dove) while latecomers should be selected to fight for a share if necessary (play Hawk). This is the basic idea of “tolerated scrounging” (Blurton Jones 1987). The harassment model, which formalized the sharing-under-pressure hypothesis, often cited in the primate literature, is a complementary approach that makes the potential costs imposed by beggars explicit in terms of reduced feeding time for owners.

Tolerated scrounging thus provides a baseline model for when we should expect sharing of resources as opposed to respect for ownership or escalated fights: sharing occurs when resources are not economically defensible by owners—the costs outweigh the benefits. The same logic can be applied to the sharing of resource patches, territories, or mates. It is important to emphasize, as Blurton Jones did, that sharing need not be preceded by overt conflict; this should only be the case when the subjective value of the food portion at stake approaches similar values for owner and latecomer (then we might start to see harassment, followed by overt conflict). So long as the value is much lower for owners than for nonowners, the optimal strategy is to be tolerant and inhibit negative responses to latecomers; hence food will be transferred without resistance. In this context, it is also crucial to note that tolerated scrounging is not incompatible with other evolutionary explanations of sharing that revolve around additional benefits to owners and may over time select for greater generosity and more active sharing.

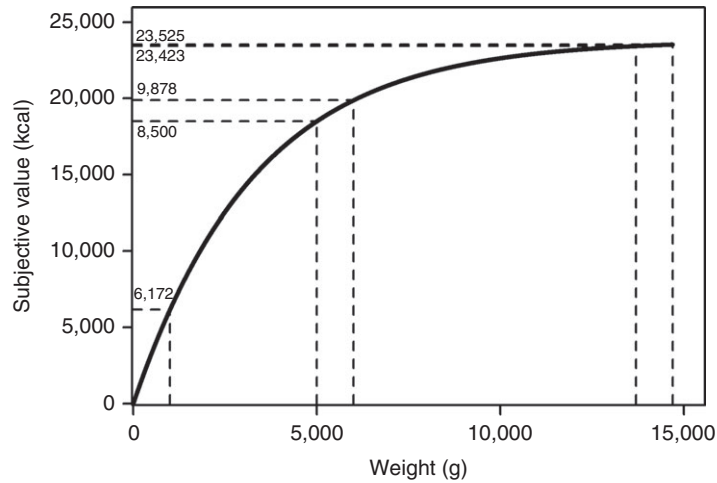


Figure 1 Diminishing returns to consumption and food sharing. The curve represents a food owner's subjective perception of the value of the package, with caloric value discounted exponentially with increasing size (here with a rate of $r = 0.0003$, which is very low; discount parameters can also differ between resources and individuals). Total package size and nutritional value are averages for collared peccaries produced by Ache foragers (taken from Kaplan and Hill 1985, tables 5 and 6). The dashed lines indicate the subjective values at certain package sizes. An owner of the entire package loses virtually no value by sharing 1 kg ($23,525 - 23,423 = 102$ kcals), whereas a nonowner gains 6,172 kcals by going from 0 to 1 kg. Even after giving away most of the package, an owner still loses much less value (e.g., going from 6 to 5 kg: $9,878 - 8,500 = 1,378$ kcals) than nonowners stand to gain. This is why nonowners should be more motivated to acquire a piece of food (play Hawk) while owners should be selected to tolerate food transfer (play Dove). This logic underlies the idea of tolerated scrounging, but the fact that owners can provide nonowners with a large benefit at minimal cost to themselves also lowers the threshold for sharing to be favored by kin selection or reciprocity.

Besides avoiding the costs of defending a resource, there are other benefits that owners might gain from sharing. There are three main hypotheses: kin selection, reciprocity, and costly signaling.

Owners can gain inclusive fitness benefits by sharing with recipients with whom they have more genes in common than with alternative recipients—that is, if the subjective cost of giving up food is lower than the subjective benefit to the recipient multiplied by the coefficient of relatedness between owner and recipient. Such kin-selected sharing is most evident in the parent–offspring context, wherein parents are often the procurers of resources that are of high value to their offspring but can also extend to the transfer of resources to other relatives. Sharing due to kin selection requires assessment of the relative costs and benefits of the resource to the owner and recipient, subject to the same logic already outlined for tolerated scrounging (see Figure 1) as well as an estimate of genetic relatedness.

If the roles of owner and nonowner are frequently reversed, or if nonowners have other services to offer, sharing may provide additional benefits accruing from reciprocity. Specifically, sharing provides additional benefits if the subjective value of the resource lost for the owner is lower than the subjective benefit provided by the recipient

at a later point, subject to discounting due to uncertainty about the future (the recipient may not be willing or able to reciprocate). For very large resources (e.g., hunted game), this threshold may be relatively low (see Figure 1), especially if subjective benefits are high (e.g., when role reversal is common and sharing buffers the risk of shortfalls, as among human foragers). In primates, role reversal may be less common as ownership of shareable resources may be biased toward dominant individuals. In this case, sharing may provide additional benefits if nonowners reliably offer services such as grooming, mating, or coalitionary support.

It is often argued that reciprocity is cognitively demanding and rare in animals (and, indeed, humans); however, these views arguably rest on unrealistic assumptions about decision-making mechanisms and on highly stringent definitions of reciprocity. Minimally, reciprocity requires, first, individual recognition and tracking of the relative value of social partners, which can be achieved by simple cognitive mechanisms such as associative learning (you like someone if they provide you with benefits, and you dislike them if they impose costs on you) and, second, an assortment of reciprocators, which can be achieved by selective association, as is commonly observed in humans and other primates. For instance, partner preferences based on past interactions (liking or disliking someone) could factor into social foraging or residential decisions, thereby producing the required assortment. This view is most consistent with the strong empirical evidence for long-term correlations between sharing food and receiving food or other benefits across human foragers and nonhuman primates (Jaeggi and Gurven 2013b), though these correlations often also hold after controlling for assortment (see next paragraph), indicating selective sharing even among those present.

Deriving additional benefits from sharing through kin selection or reciprocity requires that the owner can selectively share with relatives or reciprocating partners—that is, it requires a certain degree of control over food distribution (though see previous paragraph for how nonrandom sharing can be achieved by assortment prior to distribution). In the absence of such control, there is a problem: it may not make sense to produce a large food item in the first place if it will be subject to tolerated scrounging. In other words, the question arises as to why everyone isn't a scrounger. Kristen Hawkes and her colleagues have argued that large game is not the property of the hunter but instead constitutes a public good, open to everyone. According to this view, males are motivated to produce public goods not because of the benefits derived from sharing with particular social partners but because providing a public good conveys honest information about the producer's quality (Hawkes 1991). This information is efficiently broadcast through sharing and is then used by bystanders (who do not have to be food recipients) in future interactions (e.g., in mate choice). In short, males hunt to show off their quality and improve their mating success. This showing off, or costly signaling hypothesis, helps explain the common observation that good hunters have greater fitness.

The essence of the costly signaling hypothesis can be stated more generally: whenever behaviors can reveal honest information about underlying traits that are otherwise difficult to observe, they can impact partner choice and future social interactions. The phenotypic quality revealed in good hunters is one example, and the intention to invest

in public goods or in specific social relationships are others. As such, unobservable qualities such as hunting ability, cooperative intent, generosity, or commitment to specific partners may be signaled (i.e., made observable) through sharing and can thus inform the choice of mates, leaders, allies, friends, and foes. Note that some of these signals, such as commitment to specific partners, may again require selective sharing.

Further models that might help to better tie food-production decisions to food sharing include mutualism in cooperative production, and the cultural evolution of sharing norms. In particular, if cooperative production increases per capita return rates even when food is distributed according to tolerated scrounging, the production decision (e.g., hunt when more males are present) can be explained by mutualism. However, mutualism is not an explanation of sharing itself when food passes from owner to nonowner, as benefits are not accrued simultaneously. Sharing norms such as preferential shares for producers and their kin (see Gurven 2004 for detailed ethnographic examples) can increase the incentive to produce and reduce conflict over distribution.

Empirical tests: A brief history

Empirical tests of food-sharing models require detailed, quantitative data on food production and distribution as well as sophisticated statistical methods. Primatologists started collecting such data as far back as the 1960s but were daunted by the social complexity of sharing interactions. For instance, in his study of chimpanzee hunting and meat sharing, Geza Teleki noted that “the patterns and social regulators of distribution elude understanding” (1973, 145). Hence it fell to human behavioral ecologists, who adopted data-collection methods from animal behavior studies, to conduct the first empirical tests of evolutionary hypotheses; Hillard Kaplan and Kim Hill (1985) presented detailed data collected during eighty-one days spent on foraging trips with the Ache of Paraguay, including almost 7,000 instances of food sharing. They found support for some predictions made by the tolerated scrounging and reciprocity models.

Frans de Waal (1989) followed suit with a detailed study of more than 4,500 interactions over provisioned food among captive chimpanzees; he found strong evidence for reciprocity. De Waal also introduced matrix correlations, a statistical method developed for social interaction data that controls for repeated measures of the same individuals. Matrix correlations remained the method of choice among primatologists until mixed-effects (or multilevel) models were adopted in the late 2000s to allow for the simultaneous testing of competing hypotheses while controlling for repeated measures of individuals. Thus, state-of-the-art statistical models predicting food given from A to B include various predictors such as food received (reciprocity), relatedness (kin selection), proximity, need (e.g., family size or total household production), dominance rank, and begging intensity (all proxies for tolerated scrounging) as well as their potential interactions, all the while controlling for A’s propensity to give and B’s propensity to receive more or less than average. Most recently, human behavioral ecologists have introduced expanded multilevel models to make explicit use of their ability to model variation among individuals and dyads, thereby providing improved tests of reciprocity (Koster et al. 2015).

In terms of food production, there is still considerable debate over why individuals, males in particular, choose to produce large, shareable food items. Some argue that males' decision to hunt large game is motivated primarily by costly signaling, as they can better provide for themselves and their families by targeting food that is more predictable, comes in smaller packages, and is shared less widely. Others emphasize that foraging decisions have to be understood in the context of divisions of labor among the sexes as well as according to ability, such that specializing and overproducing followed by pooling of surplus production with others generate economies of scale and improve everyone's efficiency. Studies investigating chimpanzee hunting decisions show similar disagreements, as some emphasize ecological factors and individual nutritional gains while others conclude that social factors such as male bonding or potential mating benefits are responsible for initiating hunts (reviewed in Jaeggi and Gurven 2013a).

Clearly, these debates surrounding food-production decisions cannot be settled without knowing how food is shared; if there are predictable benefits to sharing, these should factor into the production decisions as well. A meta-analysis of twenty-five studies on food sharing among human foragers and nonhuman primates (Jaeggi and Gurven 2013b) showed significant and comparable independent effects of tolerated scrounging, kin selection, and reciprocity. Hence, owners may predictably derive benefits from sharing, and the production of large items can thus be selected for, even if food sharing appears like mere scrounging (i.e., is mostly passive and/or is initiated by harassment). Furthermore, selective association with kin and reciprocators can increase benefits to sharing even if control over actual distribution is low.

In summary, understanding food sharing requires linking selective association of individuals; production of large, shareable resources; and distribution of these resources. Various theoretical models provide explanations for each of these steps; they may often be at work simultaneously, as acknowledged by many empirical studies (Gurven and Jaeggi 2015). By explaining how individuals aim to maximize their resource access in constant negotiation with the interests of others, food-sharing models provide insights into the origins of social tolerance, generosity, and fairness reaching far beyond the domain of food.

SEE ALSO: Behavioral Ecology, Human; Behavioral Ecology, Primate; Brain Evolution and Energetics of Encephalization; Cooperation; Cooperation, Evolution of; Cooperative Child Rearing; Evolution of Alloparenting in Hominins; Costly Signaling in Human Culture; Domestic Mode of Production; Game Theory; Hunter-Gatherer Models in Human Evolution; Meat Eating in Apes and Early Hominins; Nutritional Ecology; Optimal Foraging Theory; Reciprocity; Risk and Uncertainty; Sex and Gender Roles, Division of Labor in; Sociobiology and Anthropology

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