

# Natural Cooperators: Food Sharing in Humans and Other Primates

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The study of cooperation is rich with theoretical models and laboratory experiments that have greatly advanced our knowledge of human uniqueness, but have sometimes lacked ecological validity. We therefore emphasize the need to tie discussions of human cooperation to the natural history of our species and its closest relatives, focusing on behavioral contexts best suited to reveal underlying selection pressures and evolved decision rules.<sup>1–3</sup> Food sharing is a fundamental form of cooperation that is well-studied across primates and is particularly noteworthy because of its central role in shaping evolved human life history, social organization, and cooperative psychology.<sup>1–16</sup> Here we synthesize available evidence on food sharing in humans and other primates, tracing the origins of offspring provisioning, mutualism, trade, and reciprocity throughout the primate order. While primates may gain some benefits from sharing, humans, faced with more collective action problems in a risky foraging niche, expanded on primate patterns to buffer risk and recruit mates and allies through reciprocity and signaling, and established co-evolving social norms of production and sharing. Differences in the necessity for sharing are reflected in differences in sharing psychology across species, thus helping to explain unique aspects of our evolved cooperative psychology.

primates include insects, large fruits, and vertebrate meat.<sup>7–10</sup> Among human foragers, food is commonly pooled within the nuclear family, but hunted food is shared more widely than is gathered food, and larger packages more than smaller ones.<sup>3,17–19</sup> Together, the characteristics of large package size, diminishing returns to consumption, and asynchronous acquisition produce a situation in which possessors incur only a small marginal cost by sharing, while providing a large marginal benefit to nonpossessors.<sup>20,21</sup> As such items provide a favorable cost-benefit ratio for sharing, any theoretical treatment of sharing must start with the production decisions that generate them in the first place.<sup>11</sup>

## WHAT IS FOOD SHARING?

Food sharing (henceforth: sharing) has been defined as the unresisted transfer of food from one food-motivated individual to another.<sup>7</sup> Note that this definition does not include less conspicuous forms of food-related tolerance, such as feeding in the same patch (or “co-foraging”), which may be more common than transfers among non-human primates (henceforth: primates).<sup>9</sup> Here we focus only on transfers as they feature more prominently in the literature, particularly on human foragers.<sup>3</sup>

The majority of foods shared among humans and primates come in relatively large packages that are difficult to monopolize and yield diminishing marginal returns to consumption. Also, there is asynchrony in acquisition, resulting in food possessors and nonpossessors. Common examples of shared food among wild

## LINKING FOOD PRODUCTION AND SHARING

Among human foragers, food is often transported to a central place and shared widely with group members.<sup>3,11</sup> This allows more efficient production, since individuals can forage according to their best abilities, thus overproducing certain items which, when pooled with others' production, results in greater total yield. Such economies of scale underlie the divisions of labor so integral to human societies and highlight how an individual's foraging decisions depend on those of others.<sup>11</sup> Furthermore, pooling production reduces the risk of shortfalls by smoothing consumption, especially of large, risky items.<sup>19,20</sup> Thus, sharing became an integral component of the human foraging niche by reducing risk and improving production efficiency.<sup>3,5,13</sup>

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## GLOSSARY

**Contingency** - used here strictly in the statistical sense of a positive correlation among specific individuals between giving food and receiving food or other commodities.<sup>3,33,84</sup> A necessary condition for reciprocity.

**Costly signaling** - also handicap signaling, showing off. Production and sharing is quality-dependent, thereby signaling information used by an audience in choice of mating or cooperation partners or deference from competitors.<sup>12,29</sup> Risky, widely shared items may be preferentially targeted, especially by high-quality individuals, because they maximize broadcast efficiency, whereas directed sharing may be used to signal cooperative intent to specific partners.<sup>39</sup> Requires audience or partner choice.

**Kin selection** - Food is shared preferentially with relatives if benefits to the recipient outweigh costs to the possessor multiplied by their relatedness coefficient. It is more likely when marginal costs are low (see tolerated scrounging) and benefits are disproportionately greater for recipient, such as when food constitutes critical nutritional or informational input.<sup>8,9</sup> Requires producer control.

**Mutualism** - also by-product mutualism. Occurs when collaborative production is more efficient than individual production, yet resources are distributed through tolerated scrounging.<sup>11</sup> Mutualism can account for immediate, but not delayed benefits of production.<sup>10</sup>

**Producer control** - the degree to which food producers have control over food distribution.<sup>3</sup> If absent, distributions are explained solely by

tolerated scrounging. If present, sharing can be selective and producers may gain additional benefits through kin selection or reciprocity

**Producer's share** - the portion of food consumed by its producer.<sup>11</sup>

**Reciprocity** - includes in-kind reciprocity (food for food) and trade (food for other commodities).<sup>20</sup> Used loosely here as sharing with partners who, having provided benefits in the past, are likely to do so in the future, leading to a contingency between giving and receiving over time.<sup>84</sup> This is more likely when benefits can be conferred at low cost (see tolerated scrounging). In-kind reciprocity is expected when possession of commodities is balanced over time; trade is expected when possession is consistently biased.<sup>20</sup> Requires producer control and contingency.

**Social norms** - ubiquitous in the ethnographic record, norms of production and sharing define publicly acceptable or expected contributions of labor or resources (see Gurven<sup>3</sup> for examples). Through informal sanctioning, they can help mediate conflicts of interest inherent in a risky and uncertain foraging niche.<sup>1,3</sup>

**Tolerated scrounging** - also tolerated theft, demand sharing, harassment, sharing-under-pressure. Food is shared when benefits of hoarding are outweighed by costs of monopolization.<sup>21</sup> Transfers are directed to the most persistent beggars, such as those with greater need or resource-holding potential. Given large items and diminishing returns to consumption, the marginal costs to possessors may be much smaller than the marginal benefits to recipients.<sup>21</sup>

item are often treated independently of foraging decisions.<sup>4,7,8</sup> Some foraging activities, however, predictably create opportunities for sharing. Chimpanzee hunting,<sup>24-26</sup> crop-raiding,<sup>27</sup> or foraging in patchy savannah<sup>28</sup> are all subject to scrounging because they involve multiple individuals, are highly conspicuous, and/or include transportation of food to a different location. In such contexts too, sharing is a direct consequence of production.<sup>11</sup>

## EVOLUTIONARY MODELS OF PRODUCTION AND SHARING

Various models have been put forward to explain the production of shareable food by self-interested foragers.<sup>1,3,4,7,8,10,11,19,22,23,29</sup> A broad distinction can be made between the production of public goods, the distribution of which cannot be controlled, and private goods, which can be shared selectively. When public goods are distributed according to tolerated scrounging, producers gain no benefit from sharing. However, it could still be in the individual's best interest to produce the good if the producer's share is greater than expected alternative foraging yields, which may be the case for many common instances of sharing.<sup>30</sup> In the case of collaborative production, this may be facilitated by increased efficiency through mutualism.<sup>11,31</sup> If the producer's share is smaller than alternative yields, the production of public goods cannot be explained by optimal foraging strategies, as has been argued for the hunting of large game among foragers.<sup>18</sup> In this case, costly signaling may provide an additional incentive since producers gain benefits from signaling their quality to potential mates, cooperation partners, or competitors.<sup>12,29</sup> If goods are (more) private, food distribution does not only follow tolerated scrounging, but can be preferentially directed to kin or reciprocating partners. The production and/or sharing of such goods can be explained by kin selection or reciprocity. Furthermore, directed sharing of private goods (or the eschewal thereof) can be used as a signal of cooperative intent.<sup>12,32</sup>

However, because some foods are more risky and shared more widely, some forms of production are subject to free-riding and conflicts of interest. Among humans, the question of why to share is therefore intricately linked to the question of why to

produce particular foods in the first place.<sup>3,11,17,19,22,23</sup>

Among primates, on the other hand, there is little collaborative food production or division of labor. Thus, hypotheses about sharing of the occasional nonmonopolizable

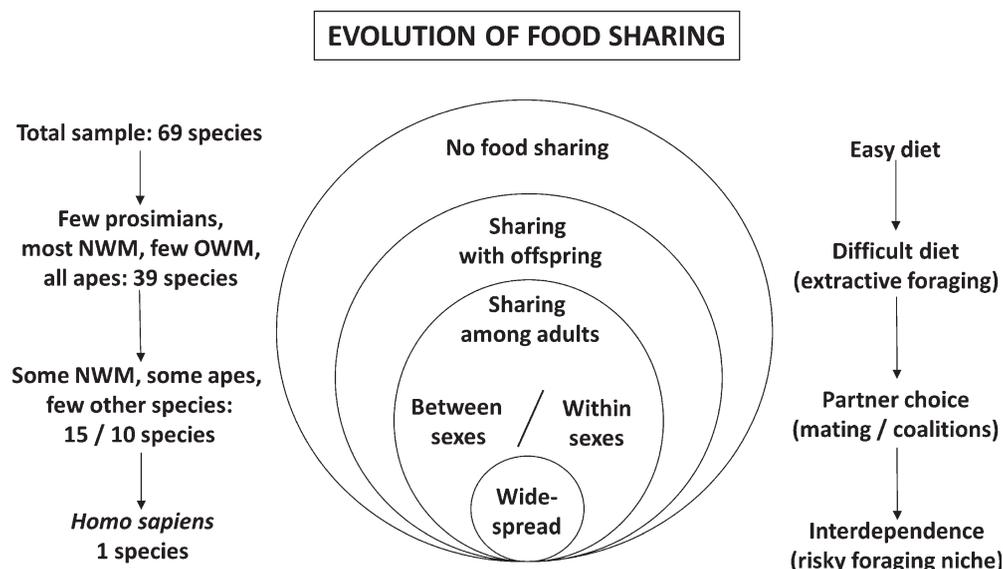


Figure 1. The layered distribution of sharing in primates. The left-hand arrows indicate ever smaller subsamples matching the relational contexts in the layers. The right-hand arrows show evolutionary transitions in other traits that co-evolved with transitions between the layers. Redrawn after Jaeggi and van Schaik.<sup>4</sup> NWM = New World monkeys, OWM = Old World monkeys.

Most commonly, shared food items are not easily monopolizable and therefore are susceptible to tolerated scrounging. However, producers may nonetheless have some control over food distribution, which is often aided or hampered by explicit social norms among human foragers. This blurs the distinction between public and private goods.<sup>3,19</sup> Further, if food lost to scroungers can buy future benefits, foraging decisions that seem inferior when considered in isolation may actually be optimal in a social foraging context with predictable sharing.<sup>11,19</sup> Whether producers gain benefits beyond tolerated scrounging therefore depends on the degree of producer control (kin selection and reciprocity), the contingency between benefits given and received (reciprocity), and the extent to which signaled information is used in partner choice (costly signaling).<sup>3</sup> Indeed, a recent meta-analysis has shown significant contingency in sharing across primate species and human populations; this contingency was comparable in effect size to tolerated scrounging and kin selection.<sup>33</sup> Such broad patterns, as well as comprehensive multi-variate analyses,<sup>34–37</sup> emphasize that since optimal strategies likely depend on context and individual quality, no single model best explains all instances of sharing.<sup>38,39</sup>

In the following we discuss explanations for sharing in more detail as we review the evidence across the primate order. We structure our review according to distinct relational contexts: from adults to immatures, among adults of different sexes, and among adults of the same sex.

## SHARING FROM ADULTS TO IMMATURES

### Primates

Sharing from adults to immatures has been reported in about half of all primate species (Fig. 1).<sup>4</sup> Because adults have the greatest control over food distribution and the majority of sharing occurs among relatives such as parents, offspring, or siblings, kin selection is a likely explanation. Two particular hypotheses of sharing due to kin-selected benefits have been proposed, the nutritional and the informational hypotheses.<sup>8</sup> Most quantitative studies to test them were conducted with New World monkeys, especially callitrichids, and great apes.<sup>7–9</sup> Sharing with offspring is rare among prosimians, with the exception of aye-ayes and tarsiers, and is conspicuously absent among many Old World monkeys, perhaps because access to nutritional and informational benefits occurs through co-

foraging rather than food transfers.<sup>4,8,9</sup>

The nutritional hypothesis proposes that infants gain substantial nutritional benefits from sharing, while parents benefit by boosting infant growth rates and facilitating weaning, thereby increasing their inclusive fitness and reproductive output (Box 1). This hypothesis predicts that sharing focuses on high-quality items and that rates of transfer are highest around weaning, but terminate soon after as investment switches to the next offspring. Among callitrichids, extensive allo-maternal care and provisioning alleviates the energetic burden of lactation on mothers, allowing them to have twin births, exceptionally high growth rates, and short interbirth intervals.<sup>8,40</sup> Food transfers focus on high-quality items and are most common around the weaning period, when immatures are almost exclusively provisioned by others.<sup>8,41,42</sup> Among great apes, on the other hand, transfers are independent of nutritional quality and peak well before weaning.<sup>43,44</sup> The nutritional hypothesis has therefore been supported for callitrichids, but not for great apes. Because sharing is relatively infrequent in other species<sup>4,8</sup> there do not seem to be major nutritional gains, although those could

### Box 1. Comparative Analyses of Food Transfers and Life-History Evolution

Comparative analyses, which control for similarity arising from shared phylogenetic or cultural history, have become increasingly common in evolutionary anthropology.<sup>92</sup> By identifying general patterns across species, these analyses can help make predictions about human evolution that can then be tested using the archeological or fossil record. Two recent applications of such methods are directly relevant to understanding the evolution of food sharing and its role in life-history evolution.

First, comparative studies of brain-size evolution across mammals show how sharing allowed the expansion of brain size during human evolution.<sup>16</sup> Because larger brains are linked to slower development and reduced reproductive rate, slowly

reproducing species like apes hit a “gray ceiling”; that is, they cannot increase brain size and bear the cost of even slower life history without falling below replacement rates of reproduction. However, allo-maternal care, in particular provisioning of offspring by fathers or other helpers, can pay for larger brains by alleviating the energetic burden on mothers.<sup>40</sup> Thus, provisioning of offspring and mothers enabled our hominid ancestors to break through the gray ceiling by dramatically shortening interbirth intervals even while expanding brain size and slowing down development relative to other apes.<sup>16</sup> This highlights how inseparably food sharing is linked to human life history.<sup>5,6,13,15</sup>

Second, a comparative study directly testing hypotheses about the

evolution of sharing in primates identified 68 species for which sharing had either been reported or was absent despite considerable study effort.<sup>4</sup> The results are summarized in Figure 1, which shows a layered distribution of sharing in primates, from species with no sharing to species sharing with offspring, as well as a subset sharing among adults of the same or different sexes, as indicated by the arrows on the left. The arrows on the right highlight other traits that co-evolved with transitions between these layers. We included *Homo sapiens* at the bottom of the figure as the only primate species to have evolved widespread sharing among adults accompanied by a high degree of economic interdependence, which is characteristic of the risky human foraging niche.<sup>5,6,13</sup>

come in the form of rare micronutrients, especially from meat.<sup>30,45,46</sup>

The informational hypothesis suggests that the main benefits to offspring are not nutritional, but consist of knowledge and experience about novel or difficult-to-process food items that they cannot yet access independently (Fig. 1). This hypothesis predicts that sharing focuses on rare and/or difficult items and is related to infants' skill levels. Callitrichid infants may profit from receiving difficult-to-process or novel items; food transfers include some of the best examples of teaching in primates.<sup>47,48</sup> In great apes, transfers focus mainly on difficult-to-process items and rates of transfer mirror infants' skill levels.<sup>43,44</sup> Similarly, capuchin infants gain access to rare or difficult food through transfers from adults.<sup>45,46,49</sup> The informational hypothesis has therefore been supported in callitrichids, capuchins, and great apes.<sup>8,9</sup>

The importance of food provisioning for maintaining fast reproductive rates in callitrichids<sup>8,9,40</sup> has selected for high sharing motivation, resulting in regular proactive transfers, high solicitation success, and more sharing of preferred food (Box 2,

Fig. 2).<sup>50</sup> Furthermore, callitrichids are the only primates to have evolved specialized calls for offering and begging.<sup>41,50</sup> In species with occasional sharing for informational benefits, mothers were selected to be tolerant, but the vast majority of transfers are passive (Fig. 2) and the offspring themselves are responsible for gathering the information they need. These differences in sharing psychology are mirrored by examples of tutoring among callitrichids,<sup>47,48</sup> but scarce evidence of teaching among other primates.<sup>51</sup>

#### Humans

The primate patterns are also relevant to understanding food transfers to human children: Extensive allo-maternal care allowed hominids, like callitrichids, to increase reproductive rates even while evolving larger brains (Box 1),<sup>16,40</sup> resulting in obligatory provisioning of mothers and offspring by fathers, siblings, or grandparents.<sup>5,15,19,52</sup> Human children, like other apes, have to learn about a difficult foraging niche in which some skills may not develop until late in life.<sup>5,13,53</sup> Further, kin-biased sharing

in humans is supported by the expansion of kin networks relative to ape-like ancestors due to pair-bonding, greater paternity certainty, and reciprocal exogamy.<sup>14</sup> Thus, intergenerational transfers among kin have become the hallmark of human social organization<sup>1,6</sup> and are inseparably linked to the evolved human life history.<sup>5,13,16</sup> Prosociality and high sharing motivation are arguably deeply rooted in this cooperative breeding system of our species,<sup>52</sup> even though family provisioning may sometimes conflict with other foraging goals.

#### SHARING AMONG ADULTS OF DIFFERENT SEXES

##### Primates

Sharing among adults exclusively evolved in species also sharing with offspring (Fig. 1) either because the latter is a precondition of the former or simply a good indicator of a foraging niche likely to contain shareable items.<sup>4</sup> Transfers from males to females are the most common form of sharing among adult primates, occurring in 15 species, more than any other

### Box 2. Sharing Psychology

Behavior is proximately regulated by evolved decision rules, or reaction norms, that on average yield adaptive outcomes.<sup>93</sup> Fine-tuned during ontogeny and subjectively experienced as emotions or motivations, these decision rules reflect solutions to recurring adaptive problems and past selection pressures.<sup>83</sup> Understanding the rules underlying food transfers (here jointly referred to as “sharing psychology”) can therefore help illuminate their ultimate functions,<sup>2</sup> as highlighted by the following examples.

Interviews among Ache and Hadza men directly tested competing hypotheses about foraging goals by giving them the choice of joining either of two fictive foraging groups.<sup>76,77</sup> Joining the group with better hunters but few unmarried women would improve family provisioning and was chosen by the majority of men; joining the group with poor hunters but many unmarried women would provide signaling and mating opportunities and was chosen only by unmarried or older men without dependent offspring among the Ache. By tapping into men’s decision-making process, such studies contribute to

arguments about foraging goals that are difficult to resolve with behavioral data alone.<sup>19,72</sup> Further advances into the study of foraging goals are likely to come from other innovative methods such as hormone-behavior interactions.<sup>94</sup>

Among primatologists, considerable debate surrounds the motivations underlying food transfers, but helpful quantifiable distinctions can be made between resisted and unresisted, passive and active transfers (Fig. 2).<sup>2,7</sup> The patterns across species indicate differential selection on traits such as inhibitory control or responsiveness to need: Among some species, there is little inhibition; food-taking is resisted or forced, suggesting no benefits to sharing. In other species, passive transfers indicate more inhibitory control by both possessors and beggars, resulting in tolerant interactions. In these cases, however, responsiveness to need seems generally low as reactive sharing is rare and occurs only in response to overt begging signals.<sup>26,56,63,66</sup> Other than human children, only callitrichids proactively sharing with infants are able to inhibit their own desire to eat even highly preferred food<sup>50</sup>;

they have evolved a specialized communication system of provisioning and begging calls<sup>47</sup> mirroring that of other cooperative breeders. Thus, the context of cooperative child care may be the clearest example of changes in sharing psychology due to strong selection pressures.<sup>52</sup> For sharing among adults, hormone-behavior interaction studies are again likely to advance debates about adaptive functions and underlying mechanisms.<sup>95</sup>

Significant advances have come from artificial experimental approaches to prosocial behavior, despite concerns about ecological validity.<sup>2,96–98</sup> For instance, economic games in human societies have shown contextual differences consistent with an evolved psychology for social exchange<sup>91</sup> that is sensitive to and shaped by co-evolving social norms.<sup>99</sup> Similar experiments with primates<sup>2,96,98</sup> have shown results consistent with the species-typical natural history of sharing, such as proactive provisioning in callitrichids and reactive helping in chimpanzees. Improved methodologies with higher ecological validity provide exciting directions for future research.<sup>100</sup>

sex-combination.<sup>4</sup> Male-female sharing is most commonly observed and studied among chimpanzees, with only few quantitative studies on other ape species,<sup>54–56</sup> Old World monkeys,<sup>57</sup> and New World monkeys.<sup>46</sup> Transfers from females to males are rarer, possibly because production and possession of shareable food are commonly male-biased<sup>24,26,27,30</sup> except in female-dominant species.<sup>54,55</sup> Adult males and females in primate groups are mostly unrelated, which precludes kin selection as an explanation. However, there are other ways in which males could benefit from sharing with females, and these differ between polygamous and monogamous mating systems.

In polygamous mating systems, male reproductive success is limited

by access to fertile females. In order to gain additional mating opportunities, males could engage in quality-dependent production of shareable food to increase their mate value (costly signaling) or trade food for mating with specific females (reciprocity). In the first case, male foraging decisions should depend on signaling opportunities such as the presence of estrous females, whereas in the second case there should be significant contingency between food given and mating received. Among chimpanzees, hunting decisions are generally unrelated to the presence of estrous females when other factors are controlled.<sup>24,25,30,58,59</sup> In no other primate species have male foraging decisions been linked to signaling opportunities. Hence, signaling oppor-

tunities to females do not seem to influence male production decisions in primates. Whether male-female sharing reflects trade or merely tolerated scrounging therefore depends on the contingency between food given and mating received.

For contingency in trade to arise, females need to have control over future mating.<sup>60</sup> In addition, the time frame may be important.<sup>59,60</sup> One context in which trade may occur on an immediate basis is during consortships. Among savannah baboons, males share meat with their current consort partners but not with females outside of consortships.<sup>57</sup> Similarly, male rhesus macaques allow females to co-feed only during consortships.<sup>61</sup> Among orangutans, female control has been

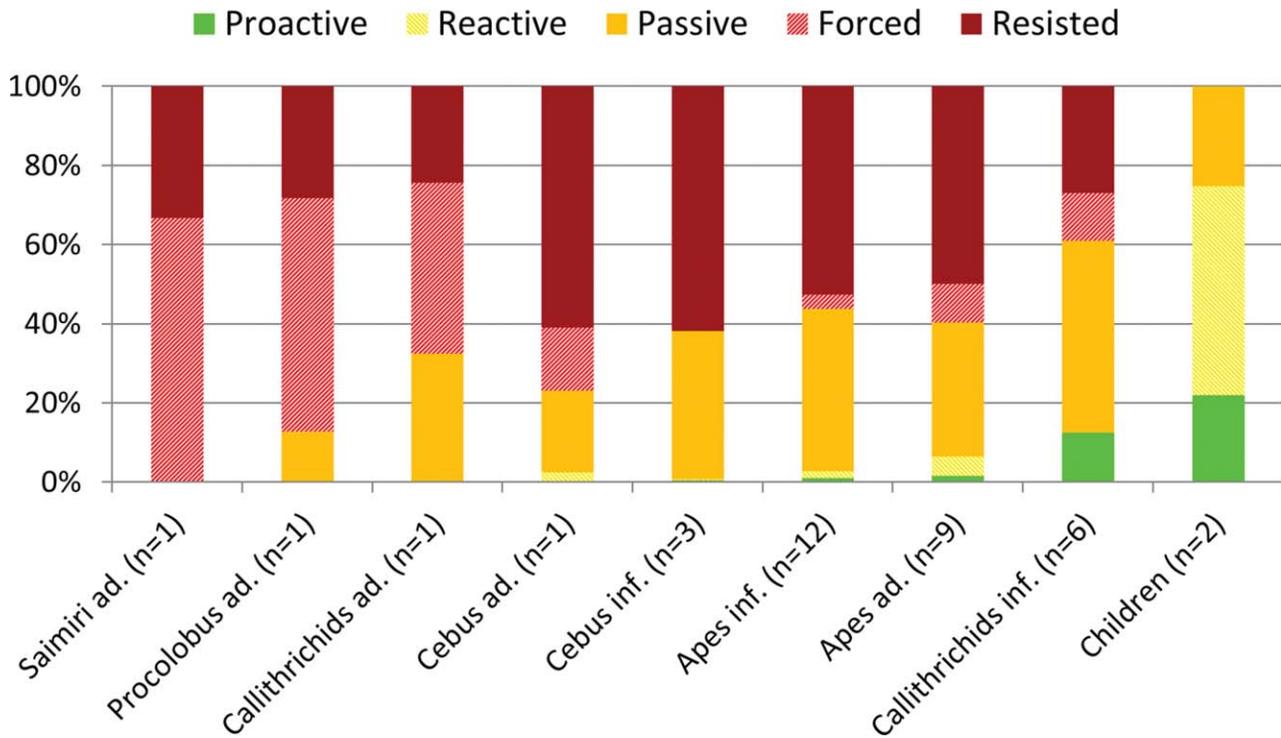


Figure 2. Outcomes of interactions over food among different species of primates and human children resulting in no transfer (resisted) or different types of transfer (forced = transfer occurs despite resistance; passive = food taken without reaction by possessor; reactive = possessor actively makes food available after request; proactive = possessor initiates transfer). ad. = sharing among adults, imm. = sharing with immatures, n = number of independent study units (publications or different populations in same publication).

demonstrated; females that have had food requests rejected by males were more likely to end the association.<sup>62</sup> These examples provide tentative evidence of how female leverage could increase male tolerance, since non-compliant males may suffer immediate costs through foregone mating opportunities. Among chimpanzees, trade seems to occur over longer time frames as males preferentially share with estrous females,<sup>27,60</sup> (but see Watts and Mitani<sup>25</sup> and Gilby<sup>63</sup>), yet there is no evidence of short-term contingency between sharing and mating.<sup>25,59,63</sup> The only support for trade among wild chimpanzees has been found on a long-term basis in a population with pronounced female choice,<sup>60</sup> which could be responsible for the discrepancy between this and other studies.<sup>64</sup> The only test for trade of food for paternity among captive chimpanzees found no positive effect.<sup>65</sup> There is some indication that primate males are more tolerant of females when immediate mating opportunities are at stake,<sup>57,61,62</sup> but whether,

in the long run, sharing consistently leads to higher mating success and greater paternity is unclear.<sup>59,60,65</sup>

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However, males may trade food with females for other commodities such as grooming and support.<sup>64</sup> There is also substantial evidence of this among captive chimpanzees.<sup>35,56,66–68</sup>

In monogamous species, males may benefit from sharing with their mates if this decreases interbirth intervals (Box 1) and if there is a good chance of siring the next offspring.<sup>69</sup> In the absence of such benefits, males should be better off eating food alone or provisioning current offspring and any male-female sharing that does occur should be explained by tolerated scrounging. Perhaps not surprisingly, then, male-female sharing is rare among many monogamous primates, although females may often have priority at feeding sites. Male-female sharing is absent in gibbons and rare in callitrichids.<sup>4</sup> Among other monogamous New World monkeys, such as titi monkeys or owl monkeys, however, transfers among mates are at least as common as transfers to offspring,<sup>4</sup> perhaps because offspring provisioning is less crucial than it is among the faster growing callitrichids. Furthermore, it has been shown that captive female owl monkeys receiving more

transfers from their mates have shorter interbirth intervals.<sup>70</sup> This mate-provisioning hypothesis is therefore tentatively supported in owl monkeys, but not in other monogamous species.

## Humans

As discussed for primate males, men could increase their reproductive success by provisioning their current partner or by gaining additional matings with other females, leading to potential conflict between these two goals.<sup>23,71,72</sup> Indeed, it has been argued that men target risky food that is widely shared at the expense of family provisioning in order to signal their quality to potential mates with maximum broadcast efficiency.<sup>18,23,29,72</sup> This strategy increases the reproductive success of good hunters,<sup>29</sup> but also increases sexual conflict with their partners.<sup>23,71</sup> This strategy should be particularly profitable for high-quality individuals who can both signal at low cost and get away with lower investment in existing partnerships.<sup>39</sup> Costly signaling can therefore help explain the links among quality-dependent food production, public generosity, and male reproductive success.<sup>12,29</sup> Trade of food for mating, on the other hand, has rarely been examined in humans.

According to a different view, even widely shared food can be an efficient choice for family provisioning, as in many societies explicit distribution norms favor the hunter's family, even when hunters do not distribute their own kills.<sup>3,19</sup> Furthermore, in contrast to primate females, women also commonly share their production with men, permitting a unique sexual division of labor that increases production efficiency through economies of scale so that foraging decisions by one sex might seem inefficient without considering decisions by the other.<sup>19,73,74</sup> Therefore, men's foraging goals may be optimal for family provisioning even with risky hunting strategies, especially since sharing outside the household may help with risk-pooling.<sup>19</sup> This view is supported by ethnographic evidence that good

hunters marry earlier and have higher reproductive success within marital unions,<sup>75</sup> as well as experiments showing that family provisioning rather than signaling opportunities is a principal motivator of foraging decisions for Hadza men and Ache men with dependent offspring (Box 2).<sup>76,77</sup>

## SHARING AMONG ADULTS OF THE SAME SEX

### Primates

Sharing among same-sex individuals has been reported in 10 species (Fig. 1), including some apes and New World monkeys, especially captive capuchins. It is most commonly observed as male-male sharing, although transfers among females also occur.<sup>4</sup> As with sharing between

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**... sharing between (human) families is essential to buffer risk in an unpredictable foraging niche where individual families may go through extended periods of net consumption even while adults are at their productive peaks.**

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the sexes, this male bias may be due to biased production and possession of shareable food in male-dominant species.<sup>24-28,30,46</sup> Both males and females could benefit from sharing among themselves when production and sharing signal qualities desired by cooperation partners or deferred to by rivals (costly signaling) or when recipients are related (kin selection) or likely to provide benefits in the future (reciprocity), either as in-kind reciprocity or trade for other commodities.<sup>20</sup> Most quantitative tests of these hypotheses found evidence for kin-biased sharing,<sup>33</sup> but the question of benefits from sharing with non-kin is more contested.

It has been suggested that chimpanzee males hunt and subsequently share with allies to gain coalitionary support.<sup>24,25,78,79</sup> Several studies found that hunting decisions depended on the number of adult males present,<sup>24,25,80</sup> but others found no effect of the presence of males in general<sup>58</sup> or preferred grooming partners in particular.<sup>30</sup> Alternative to male bonding, hunting could therefore be explained by individual foraging goals such as direct nutritional gains,<sup>30,58</sup> perhaps facilitated by mutualism due to cooperative production efficiency.<sup>31</sup> Nonetheless, several studies found significant contingency between transfers given and other commodities received.<sup>24,25,33,64,79</sup> This has been corroborated by studies in captivity<sup>35,56</sup> and suggests selective sharing with reciprocating partners. Thus, even though social factors may predict chimpanzee hunting only insofar as they increase production efficiency through mutualism, hunters may nonetheless gain benefits from selective sharing with allies.

Similarly, female chimpanzees rarely produce large shareable items in the wild, but exchange food for grooming and support when given the opportunity in captivity and in the wild.<sup>33,56,64,66,67</sup> Female capuchins share food reciprocally in captive experiments<sup>81,82</sup> despite sharing only rarely in the wild.<sup>46</sup> This suggests that a need for partners in other contexts such as coalitionary support selected for higher tolerance toward valuable partners, which is manifested as selective sharing. Alternatively, closer social partners may simply be more likely than others to approach possessors and acquire food through tolerated scrounging, regardless of the possessors' inclination to share. Either way, we expect to find contingency between sharing and receiving other benefits in any species in which social bonds are formed and shareable food is encountered or provided.<sup>4</sup>

While passive transfers among adult primates (Fig. 2) may reflect either tolerance toward specific partners or tolerated scrounging, possessors could take a more direct role in

food distribution through active transfers,<sup>35</sup> which may include large portions of meat.<sup>26</sup> By directing transfers to partners who have provided benefits in the past, possessors could thus gain benefits through reciprocity.<sup>2,68,83,84</sup> The value of social partners is likely encoded in the brain as a compressed score of the relationship history, which modulates sharing psychology so that more valuable partners are more likely to elicit a positive response such as tolerance or active sharing.<sup>2,83</sup> Across species, varying need for social partners should result in different sharing psychology,<sup>2</sup> as exemplified by differences between closely related species in comparable experiments: While bonobos showed no contingency, few tolerated transfers and no active transfers of monopolized food in two studies, chimpanzees shared more actively, tolerantly, and reciprocally, mirroring a greater need for allies.<sup>56</sup> Thus, species differences in sharing psychology may allow inferences about past selection pressures (Box 2).

## Humans

It has been suggested that, like primates, both men and women in foraging societies gain social support from signaling or sharing,<sup>85–87</sup> which sometimes is referred to as disability or health insurance affordable to high producers that may only occasionally be cashed in.<sup>5,88</sup> Such support, especially during periods of sickness or disability, substantially lowers mortality rates among foragers, helping to explain the longer life-span in humans.<sup>5</sup> Support may be recruited by signaling quality and cooperative intent through production and sharing<sup>12,32</sup> or trade for food. As with costly signaling to attract mates, targeting risky, widely shared food to maximize broadcast efficiency may conflict with family provisioning goals<sup>89</sup> unless social support increases offspring survival within marital unions.<sup>29,85</sup>

Whether by investing in social capital through the contribution of public goods<sup>12,18,23,89</sup> or through more directed transfers among kin or reciprocating partners,<sup>3,17,19,20</sup> shar-

ing between families is essential to buffer risk in an unpredictable foraging niche where individual families may go through extended periods of net consumption even while adults are at their productive peaks.<sup>1,5,37</sup> Many studies have therefore examined whether sharing food with particular others is reciprocated in kind. This possibility was supported by a recent meta-analysis showing significant, albeit low contingency between food given and received across human populations.<sup>33</sup> Furthermore, the free-rider problems characteristic of social foraging, the uncertainty of food production and expected family size (and therefore relative need), and the different levels of productivity and roles across the life span may have necessitated the negotiation of social norms to mediate conflicts of interest in production and sharing.<sup>1,3</sup> For instance, pregnant women in many foraging populations receive preferential meat shares despite their reduced productivity; also, younger families are supported by older ones and larger families by smaller ones. Norms of production and sharing among foragers thus resemble social contracts established under a Rawlsian veil of ignorance about future need.<sup>90</sup>

In contrast to primates, much human sharing is voluntary and proactive (Fig. 2), which is consistent with generosity as an honest signal of cooperative intent, as well as higher dependence on social partners, either for risk-buffering or support. As among primates, repeated beneficial interactions should lead to the formation of long-term relationships or social bonds with mechanisms to negotiate exchange and discourage cheating within such relationships.<sup>3,39,83,84,91</sup> Further, social norms of production and sharing in foraging societies act as focal points that help define the value of particular contributions. Public understanding of these norms may help reduce the costs of punishment and potential retaliation by defectors.<sup>1,3</sup>

## CONCLUSIONS

In summary, many primates forage largely for their own needs, with

little systematic sharing. If transfers do occur, they can often be explained by tolerated scrounging. In some species, benefits from sharing can nonetheless be high, as they are among cooperatively breeding callitrichids, and have led to extensive, proactive provisioning; in other species, benefits are lower and merely reflected by passive tolerance. Among adult primates, some hypotheses have mixed empirical support, such as trade of food for mating between males and females. In other cases, sharing is consistently associated with other benefits received, suggesting selective sharing with valuable social partners. These differences in benefits gained from sharing, or costs incurred from not sharing, are reflected in species differences in sharing psychology (Box 2, Fig. 2).<sup>2</sup>

Among human foragers, the reliance on sharing, with its manifold benefits, is greater than in any other primate species. Sharing is a critical component of allo-parenting and intergenerational cooperation, contributing to greater reproductive success by facilitating faster reproduction and greater survival (Box 1).<sup>5</sup> Humans exhibit all primate patterns of sharing and expand provisioning to span multiple generations in extended kin networks; signal their quality as mates and social partners by producing risky, widely shared items; and use sharing with kin and reciprocating partners to buffer risk and increase production efficiency through divisions of labor and economies of scale in a highly interdependent foraging niche. This heavier reliance on provisioning, signaling, and social exchange to solve multiple adaptive problems can help explain unique aspects of human cooperative psychology such as high levels of generosity, sensitivity to signs or signals of need, or audience effects.<sup>2,3,12</sup> In addition, the necessity of solving collective action problems inherent to the human foraging niche may have been a major driver for the establishment and co-evolution of social norms.<sup>1</sup>

In conclusion, the production and sharing of food provides an important context for the study of

cooperation, illuminating how selection pressures underlying the natural history of a species shaped behavior and psychology. Further exploration of the origins of human traits in other primates and identification of their correlates across species can help us understand changes that occurred during human evolution and how these may be traced in the archeological and fossil record.

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