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Chimpanzees share food for many reasons: the role of kinship, reciprocity, social bonds and harassment on food transfers

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There is currently great interest in the phylogenetic origins of altruistic behaviour within the primate order. Considerable attention has been focused on chimpanzees, *Pan troglodytes*, because they are our closest living relatives and participate in a wide range of collective activities, including hunting and food sharing. Food sharing is of particular importance because it plays a critical role in the human foraging niche, but food sharing among adults is rare in nonhuman primates. Some research suggests that chimpanzees selectively share meat with reciprocating partners and allies, while other work indicates that chimpanzees primarily share to reduce harassment from other group members (tolerated theft). We examined the effects of kinship, relationship quality, reciprocity and the intensity of solicitations on the pattern of food transfers in six captive groups of chimpanzees. We observed events that occurred after the chimpanzees were provisioned with large frozen juice disks. These disks share some properties with prey carcasses: they are a valued, but limited, resource; they take a considerable period of time to consume; they can be monopolized by one individual, but bits can be broken off and transferred to others. Our analyses suggest that food transfers serve multiple functions for chimpanzees. Individuals may use food transfers to enhance the welfare of closely related group members, strengthen social relationships with favoured partners and reduce the costs of persistent solicitations.

Humans form larger, more complex and more cooperative societies than other vertebrate taxa, and this has generated interest in how we came to be such unusual creatures (Burkhart et al. 2009; Warneken & Tomasello 2009; Silk & Boyd 2010). Efforts to understand the phylogenetic origins of cooperation within the human lineage have focused on chimpanzees, *Pan troglodytes*, for several important reasons. First, chimpanzees are our closest living relatives. Second, chimpanzees participate in a wider range of collective activities than most other nonhuman primates. In the wild, male chimpanzees groom one another, form coalitions, jointly defend access to mates and patrol the borders of their territories (Muller & Mitani 2005). Female chimpanzees are less gregarious than males, but form lasting social bonds with other females (Boesch & Boesch-Achermann 2000; Gilby & Wrangham 2008; Langergraber et al. 2009). Adult females often share food with their offspring, particularly foods that are difficult for their offspring to procure or process on their own (McGrew 1975; Silk 1978; Nishida & Turner 1996). Third, chimpanzees are the only nonhuman primate species in which food is regularly shared among adults in the wild (Jaeggi & van Schaik 2011). Food sharing among chimpanzees is of particular interest because food sharing is a universal feature of human societies and plays a critical role in the human foraging niche (Kaplan et al. 2009).

Food sharing also occurs outside the primate order (Stevens & Gilby 2004). For example, males sometimes provide resources to prospective mates during courtship, carnivores sometimes hunt together and share access to kills, and in cooperatively breeding species, breeding females are sometimes provisioned by other group members. Although reciprocity and kin selection are most often invoked to explain food sharing, Stevens & Gilby (2004) emphasized the importance of others factors, such as by-product mutualism and group augmentation. They also discussed the possibility that food sharing may sometimes be a form of tolerated theft (Blurton Jones 1984; Moore 1984) or sharing under pressure (Wrangham 1975; Stevens & Stephens 2002; Stevens & Gilby 2004), as possessors share food in order to reduce the costs of defending resources against rivals.

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Adult chimpanzees frequently hunt monkeys and small mammals, regularly share meat from the carcasses of captured prey (Muller & Mitani 2005) and occasionally share plant foods with other adults (McGrew 1975; Slocombe & Newton-Fisher 2005; Hockings et al. 2011). The evolutionary forces shaping food transfers among chimpanzees are the subject of much discussion. In the Taï Forest of Côte d'Ivoire and in Ngogo in the Kibale Forest of Uganda, males selectively transfer meat to males that have also transferred meat to them and to males that support them in agonistic interactions (Mitani & Watts 1999, 2001; Boesch & Boesch-Achermann 2000; Mitani 2006). Reciprocal transfers of plant foods have also been documented in captive chimpanzees (de Waal 1989, 1997; Jaeggi et al. 2010a). However, among chimpanzees at the Gombe Stream in Tanzania, Gilby (2006) found no correlation between meat transfer and grooming or proximity within dyads. He argued that males at Gombe give up parts of their kills 'to avoid the costs of defending a food item against persistent beggars'. Thus, food transfers may be a form of tolerated theft (Blurton Jones 1984) or sharing under pressure (Wrangham 1975; Stevens & Stephens 2002; Stevens & Gilby 2004).

There have also been reports that males exchange meat for sex with receptive females. Such transfers have been reported to enhance immediate mating opportunities at Gombe (Stanford 1998) and future mating prospects, but not immediate ones, in the Taï Forest (Gomes & Boesch 2011). However, in a detailed review of patterns of food transfers and mating behaviour at several east African sites (Gombe, Kanyawara, Ngogo), Gilby et al. (2010) found no evidence that the presence of oestrous females increased the likelihood that males would hunt or preferentially transfer meat to receptive females, or that food transfers enhanced males' short-term mating success. They concluded that 'meat transfers in chimpanzees are rarely sexually motivated' (page 51).

Although these studies provide very different interpretations of food transfers in chimpanzees, they are not necessarily incompatible. It is possible that food transfers may serve different functions in different contexts. Some food transfers may enhance the welfare of closely related group members, while others may strengthen alliances with favoured partners or enhance future mating prospects. In some cases, food transfers may reflect a trade-off between the benefits of monopolizing food items and the costs of defending them. Transfers may be made after persistent solicitations, but if possessors control the distribution of food, they may still be able to direct transfers selectively to reciprocating partners (Gurven 2004; Jaeggi et al. 2010a, b).

Here we examine the effects of kinship, relationship quality, reciprocity and the intensity of solicitations on the pattern of food transfers in six captive groups of chimpanzees. Our analyses focus on events that occurred after the chimpanzees were provisioned with large (30.5 × 12.5 cm) frozen juice disks. These frozen disks share some properties with prey carcasses: they are a valued, but limited, resource because only two or three are provided at one time to the group; they take considerable time to consume; they can be monopolized by one individual, but portions can be detached and transferred to other individuals, and more than one individual can feed on a disk at the same time.

METHODS

The study was conducted at the Michale E. Keeling Center for Comparative Medicine and Research (Bastrop, TX, U.S.A.). We observed all members of six groups that were housed in large outdoor compounds (22.86 m in diameter for a total of area of 410.25 m^2) connected to indoor enclosures. The outdoor compounds contained enrichment devices (e.g. climbing structures, ropes and swings, barrels, and other toys). The chimpanzees had ad libitum access to primate chow and water during the day. Each group also received fruit and vegetable feeds four times per day, as well as additional food and material enrichment several times per week. The animals spent the majority of their time in the outdoor compounds, and during observations, the doors to the indoor enclosures were closed so that all chimpanzees in the group remained outside and in view.

The study groups ranged in size from 7 to 14 individuals (Table 1). The composition of social groups was stable over the course of our study, and most individuals had lived in the same group since the late 1970s. There were few young infants or juveniles in the study groups because females had been fitted with contraceptive devices to prevent conception. None of the females were pregnant or lactating during the study period, and all but five of the adult females were cycling. Information about kinship, dominance rank and female reproductive status were obtained from colony records.

Pant-grunts are submissive vocalizations that provide a clear indicator of dominance and subordinance in chimpanzees (Wroblewski et al. 2009). In the study population, pant-grunt vocalizations were monitored during social introductions and periods of high activity such as feeding and enrichment distribution. Individuals that received pant-grunts from all other same-sexed individuals and never directed them at other same-sexed individuals were categorized as high-ranking. Individuals that both pant-grunted to other same-sex individuals and received pant-grunts from other same-sex individuals were classified as middle-ranking. Individuals that pant-grunted to other same-sex individuals, but never received pant grunts from other same-sex individuals were categorized as low-ranking.

The groups included 28 mother–offspring pairs, 11 pairs of siblings (3 male–male, 6 male–female and 2 female–female pairs), three grandmother–grand-offspring dyads, and one uncle–niece dyad. Paternal relatedness was not known for all dyads and is not included in the analyses. For the purposes of these analyses, we assumed that siblings were related by 0.25 and that the single uncle–niece dyad was related by 0.125.

Observations of Food Transfers

We monitored events that occurred after the chimpanzees were provisioned with frozen juice disks. The disks were made by mixing fruit juice, water and peanuts together and freezing them in a round mould, which measured approximately 30.5 cm in diameter. The disks were removed from the mould before they were given to the chimpanzees. The chimpanzees were familiar with frozen juice as an enrichment treat. However, during the period of testing, frozen juice was not given as enrichment in order to maximize interest in the disks. Groups that contained seven to nine individuals were provisioned with two disks, and groups that contained at least 10 individuals were provisioned with three disks.

Table 1
Demographic composition of the six chimpanzee study groups

Group	Adult male	Subadult male	Adult female	Subadult female	Immature	Total
C2	2	4	6	0	2	14
C3	1	2	5	3	1	12
C4	3	1	6	0	1	11
C5	1	1	5	0	0	7
C6	2	1	4	1	0	8
C8	1	1	7	0	1	10

Definitions of age–sex categories based on Goodall (1986): adult male ≥16 years; adult female ≥14 years; subadult male 8–15 years; subadult female 8–13 years; immature <8 years.