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REVIEW

A conceptual framework for nonkin food sharing: timing and currency of benefits

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Many animal species, from arthropods to apes, share food. This paper presents a new framework that categorizes nonkin food sharing according to two axes: (1) the interval between sharing and receiving the benefits of sharing, and (2) the currency units in which benefits accrue to the sharer (especially food versus nonfood). Sharers can obtain immediate benefits from increased foraging efficiency, predation avoidance, mate provisioning, or manipulative mutualism. Reciprocity, trade, status enhancement and group augmentation can delay benefits. When benefits are delayed or when food is exchanged for nonfood benefits, maintaining sharing can become more difficult because animals face discounting and currency conversion problems. Explanations that involve delayed or nonfood benefits may require specialized adaptations to account for timing and currency-exchange problems. The immediate, selfish fitness benefits that a sharer may gain through by-product or manipulative mutualism, however, apply to various food-sharing situations across many species and may provide a simpler, more general explanation of sharing.

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Sharing food appears to exemplify the paradox of altruism: a recipient gains fitness benefits at the expense of a donor. Despite this apparent altruism, food sharing commonly occurs in nonhuman animals, including insects (Bolten et al. 1983; Boggs 1995; Vahed 1998), birds (Heinrich 1988a; Stacey & Koenig 1990; Thiollay 1991; Evans & Marler 1994), cetaceans (Johnson 1982; Hoelzel 1991), vampire bats, *Desmodus rotundus* (Wilkinson 1984; Denault & McFarlane 1995), and other small mammals (Judd & Sherman 1996; Brotherton et al. 2001). Primates, in particular, have been well studied (reviewed by Feistner & McGrew 1989), including prosimians (Gurksy 2000), New World monkeys (Starin 1978; Ferrari 1987; Feistner & Price 1990; Perry & Rose 1994; Pastor-Nieto 2001), Old World monkeys (Kavanagh 1972; Strum 1975, 1981; Dittus 1984) and apes (Kuroda 1984; de Waal 1989; Nettelbeck 1998). Many of these and other authors have used different definitions of food sharing. Here, we adopt a relatively broad definition of sharing: joint use of monopolizable food items. That is, if an individual can defend a food item but allows another individual to consume part of the item, it is considered to be sharing.

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This definition includes both passive (tolerated theft) and active sharing (facilitated transfer, food recruitment). Regardless of the method of transfer, the food owner loses potential fitness benefits by sharing.

Sharing poses an important economic problem in animal societies. Although apparently altruistic, sharing typically yields benefits to the food donor either indirectly through kin selection (Hamilton 1964) or directly through other mechanisms. Much of animal food sharing probably results from kin selection or parent–offspring sharing (Feistner & McGrew 1989). Because this type of sharing is well understood, we focus on nonkin explanations of sharing involving direct fitness benefits to the donor.

Fitness Benefits

Here we review nonkin sharing studies using a conceptual framework partially based on Brown's (1980) fitness components. We divide fitness benefits for nonkin sharing along two axes (Table 1). Our first axis considers the time at which the donor receives its benefit: either immediately following sharing or after a delay. For example, a lioness, *Panthera leo*, that just captured a Thompson's gazelle, *Gazella thomsonii*, has two options when another pride member approaches: she can defend the carcass or allow the intruding lioness to feed with her. By sharing, the owner may benefit immediately by avoiding a contest,

Table 1. Summary of hypotheses and examples of food sharing categorized by timing and currency of benefits

	Immediate benefits			Delayed benefits			
	Explanation	Species	Studies	Explanation	Species	Studies	
Food for food	Increased foraging	Ravens	Heinrich 1988a, b, 1989	Reciprocity	Vampire bats	Wilkinson 1984; Denault & McFarlane 1995	
		Hyaenas Killer whales	East & Hofer 1991 Hoelzel 1991; Guinet et al. 2000		Capuchin monkeys Chimpanzees	de Waal 1997b, 2000 de Waal 1989; Mitani & Watts 1999, 2001	
Food for nonfood benefits	Predation avoidance	House sparrows	Elgar 1986	Trade	Vampire bats Capuchin monkeys Chimpanzees	Wilkinson 1986 Westergaard & Suomi 1997 de Waal 1989, 1997a; Koyama & Dunbar 1996	
		Mate provisioning	Insects		Boggs 1995; Gwynne 1997; Vahed 1998 Stanford 1998	Status enhancement	Arabian babblers
	Harassment	Chimpanzees				Chimpanzees	Boesch & Boesch 1989
		Rhesus monkeys Chimpanzees	Hauser 1992 Wrangham 1975; Goodall 1986	Group augmentation	Scrub-jays Meerkats	Woolfenden & Fitzpatrick 1978; Brown 1980, 1987 Clutton-Brock 2002	

which could result in the loss of the entire carcass or injury to the owner. Alternatively, sharing may provide delayed benefits by increasing the survival of the intruding female, thereby raising the chances that she remains in the group. If larger groups of females can better defend their cubs from infanticidal males, the lioness may reap future rewards for sharing.

Categorizing types of sharing by the time at which the fitness benefit accrues (immediate or delayed) provides an important distinction. Deferring immediately obtainable benefits until the future has two primary difficulties. First, delaying benefits trades current fitness for future fitness. Animals can invest current resources into offspring, but by delaying benefits, they divert investment into future offspring. If this delays reproduction, it could reduce lifetime reproductive success. Second, much can happen between the time that a food item is shared and the return benefit accrues. Because of this uncertainty, animals may discount the value of delayed benefits (Mazur 1987; Rachlin 2000), thus increasing the perceived value of immediate benefits. That is, animals may prefer smaller, immediate benefits to larger, delayed benefits. This preference may cause animals to devalue food up to 50% in the first second of delay (Mazur 2000). Discounting plays an important role in food sharing because food items are often ephemeral (Stephens & Krebs 1986). Explanations that rely on these delayed benefits may require complicated mechanisms to overcome the problem of discounting.

Our second axis considers the fitness currency of the benefit received by the donor. The donor can either receive more food as a result of sharing or receive another type of benefit such as grooming, predation avoidance, or mating opportunities. In the lion example, the owner that shares to avoid the contest and possible loss of the carcass gives up part of her food to consume more food: the returned benefit currency is the same. Yet, the owner that

shares to maintain a large group size exchanges food for another currency: increased cub survival.

Classifying fitness effects based on the currency of the received benefit allows us to consider whether the food donors must convert between fitness currencies (the biological market effect: Noë & Hammerstein 1994, 1995; Noë et al. 2001). How does one bite of food convert into decreasing predation risk, increasing the probability of mating, reducing harassment costs, lowering parasite load, acquiring higher rank, or increasing group size? We do not suggest that animals consciously calculate these conversions; rather, natural selection favours individuals that make appropriate conversions. Nevertheless, variation in amounts of food donated and values of returned benefits may require flexible, complicated rules to convert between variable benefits. Some argue that the complexity of these trading networks drove the evolution of the human brain (La Cerra & Bingham 1998).

Despite the importance of timing and currency on fitness, few studies have satisfactorily considered these aspects in food sharing. We argue that these factors influence the complexity of hypotheses used to explain sharing. Therefore, this framework can help us evaluate which hypotheses provide the most parsimonious explanations of sharing.

IMMEDIATE BENEFITS

Immediate benefits accrue during or directly following the sharing event. Occasionally, classifying benefits as immediate or delayed proves difficult; some types of benefits can seem to occur both immediately and after a delay. Nevertheless, a clear difference often distinguishes between benefits that accrue during or immediately following sharing and those that accrue after a time delay.

Food for Food

Increased foraging efficiency

Although it may appear to be counterintuitive, individuals may actually increase their foraging efficiency by sharing food with other individuals. This occurs most often through recruitment calling. In some species, individuals that have information about the location of food give specific calls that attract nearby foragers. The callers do not necessarily possess food but alert others to the location of food, effectively sharing food.

Richner & Heeb (1995, 1996) proposed the 'recruitment centre' hypothesis as a selfish alternative to Ward & Zahavi's (1973) altruistic 'information centre' explanation of communal roosts. Richner & Heeb contended that recruitment calling actually benefits the caller by immediately increasing its capture rate. Brown et al. (1991) supported this claim by observing that cliff swallows, *Hirundo pyrrhonota*, attract conspecifics with food calls. Because individuals in a group have higher prey capture rates than singletons (Brown & Brown 1996), callers may recruit group members to increase individual foraging efficiency. Larger group sizes may also lower individual vigilance for predators (Lima & Dill 1990), thereby allowing more time for foraging.

In addition to increasing baseline capture rate, recruiting can allow individuals to form groups that displace food owners, thereby providing access to otherwise inaccessible food sources. Probably one of the most celebrated cases of this is raven, *Corvus corax*, recruitment calling at large carcasses. Heinrich and colleagues (Heinrich 1988a, b, 1989; Heinrich & Marzluff 1991, 1995) described situations in which juvenile ravens give recruitment calls before feeding at large carcasses. After eliminating reciprocal altruism and kin selection as possible explanations (Heinrich 1988b; Marzluff & Heinrich 1991; Parker et al. 1994), Heinrich and colleagues proposed that by-product mutualism (West-Eberhard 1975; Brown 1983) probably explains the sharing. By recruiting other ravens, juveniles can overwhelm the defences of adult territory holders, thereby gaining access to the otherwise inaccessible carcass (Heinrich 1988a, 1989).

By increasing call rate as they approach lions at a kill, spotted hyaenas, *Crocuta crocuta*, also appear to recruit others to take over a carcass (Holekamp et al. 2000). Larger group sizes allow them to supplant nonclan members as well as other species such as lions and leopards, *Panthera pardus* (East & Hofer 1991). Although lions may not actively recruit other pride members when defending a carcass from hyaenas (C. Packer, personal communication), sharing with pride members may allow them to defend their kill more effectively, thereby reducing their chances of losing the entire kill (Cooper 1991).

Killer whales, *Orcinus orca*, may increase their foraging efficiency by sharing the carcasses of pinnipeds and other cetaceans (Hoelzel 1991; Guinet et al. 2000). Guinet et al. (2000) hypothesized that they may share to maintain buoyancy of large carcasses. If a single killer whale feeds solitarily, the carcass may quickly sink in deep water. By sharing, multiple whales can keep the carcass afloat, allowing individual foragers to consume more.

Food for Nonfood Benefits

Predation avoidance

In addition to increasing capture rate, recruitment calling may yield immediate benefits in a currency other than food, such as reduced predation risk. By recruiting others, an individual feeds in a group rather than solitarily, potentially diluting predation risk, increasing predator detection, and confusing predators (Lima & Dill 1990; Krause & Ruxton 2002). Elgar (1986) found that house sparrows, *Passer domesticus*, give more recruitment calls in the presence of divisible food; however, call rate decreases dramatically as flock size increases. This suggests that the birds may recruit others to dilute their own predation risk only when food is shareable and risk is high for solitary foragers.

Models of sharing under predation risk predict that sharing/recruiting can immediately benefit individuals through predation avoidance. Newman & Caraco (1989) modelled recruitment calling situations in which risk of starvation and group predation risk vary. Recruiting is evolutionarily stable when predation risk decreases with group size; therefore, calling benefits solitary individuals by increasing group size and diluting risk. In another set of models, provisioning unrelated offspring at a nearby nest quiets begging calls, thereby reducing the chance of attracting predators. By sharing with unrelated offspring, an individual may decrease predation risk for its own young (Caraco & Brown 1986; Giraldeau & Caraco 2000).

Mate provisioning

In many species of insects, birds and mammals, males acquire and donate food to females either before, during, or after copulation (termed mate provisioning, courtship feeding, nuptial gift giving, or meat-for-sex). Males may relinquish body parts, produce glandular secretions, or share prey or other food to gain fitness benefits via natural and sexual selection (reviewed in Lack 1940; Thornhill 1976; Boggs 1995; Gwynne 1997; Vahed 1998).

Naturally selected fitness benefits of mate provisioning act primarily on survival. In several insect species, females cannibalize males during or after copulation. Provisioning the female may distract her from cannibalizing the male, thereby increasing his probability of survival and facilitating the transfer of sperm (Gwynne 1997). Provisioning may also offer paternal investment by providing nutritional support for the female. Providing food has a direct effect on female fecundity in many species of insects and birds by increasing egg number, egg size and offspring weight (Nisbet 1973; Newton 1979; Gwynne 1982; Lifjeld & Slagsvold 1986; Moore et al. 2000).

Sexual selection may also maintain mate provisioning via sperm competition and female choice. Males of many insect species donate an edible gelatinous mass (spermatophylax) in addition to a sperm sac during mating. Sakaluk (1984) suggested that provisioning female crickets, *Gryllodes supplicans*, allows enough time for the ejaculate to transfer out of the sperm sac before she can feed on the sperm. Other researchers propose that the spermatophylax may prevent future mating by releasing

refractory chemicals, plugging or filling the reproductive tract, or releasing chemicals that render foreign sperm inviable (Gwynne 1986). Probably the most common explanation of mate provisioning is mate attraction. Males share food with females to entice them to mate, and sharing may signal the male's fitness and paternal investment. Feeding females often increases copulation rate (Tasker & Mills 1981; Vahed 1998; Mougeot 2000; González-Solís et al. 2001) and mate retention (Tasker & Mills 1981) in insects and birds.

In chimpanzees, *Pan troglodytes*, males capture monkeys and may give meat to females, possibly in exchange for mating access (meat-for-sex hypothesis). A male chimpanzee may occasionally withhold meat from a sexually receptive female until he has mated with her, and only then allow her to obtain a portion (Goodall 1986; Stanford 1998). Sexually receptive females may receive more meat from males than expected by chance (Teleki 1973, 1981). Stanford and others (Stanford et al. 1994; Stanford 1998) interpreted this as evidence that males trade meat for mating. However, Goodall (1986) and Teleki (1973, 1981) demonstrated that sexually receptive females are more persistent in their efforts to obtain meat (i.e. high harassment), possibly explaining their increased success. Kuroda (1984) showed that female bonobos, *Pan paniscus*, obtain more food from males if they first copulate with them.

Other studies of chimpanzees have failed to find a relationship between food and mating, instead finding no preferences for sexually receptive females (I. C. Gilby, unpublished data) or, more importantly, no effect of sharing on male reproductive success (Hemelrijk et al. 1992, 1999; Mitani & Watts 2001). Rather than sharing in return for an immediate copulation, a male chimpanzee may share to establish an affiliative relationship with a female, increasing the chances of mating later. In the chimpanzees at Gombe National Park, Tanzania, a male's frequency of involvement in consortships (exclusive mating relationships) positively correlates with the frequency with which he shares food with females (Tutin 1979). However, it remains unknown whether sharing with a particular female increases the chances of consorting with that female. This possibility of future rewards suggests that mate provisioning can provide both immediate and delayed benefits.

Harassment and manipulative mutualism

Sharing may occur because begging reduces the fitness of the owner. Owners benefit by sharing part of the food with the beggar to avoid injury and energetic or opportunity costs. Blurton Jones (1984, 1986, 1987) proposed the 'tolerated theft' hypothesis for sharing, contending that if the fitness benefit of consuming a packet of food follows a diminishing returns function, later bites of food provide less fitness benefit than earlier bites. Therefore, if a hungry beggar encounters a partially satiated owner, an asymmetry in hunger level exists. Parker's (1974) model predicted that individuals that gain more from a resource should fight more vigorously, forcing the partially satiated owner to acquiesce and share with the beggar. Other

theoretical (Winterhalder 1996b) and observational (Kuroda 1984; Goodall 1986; Perry & Rose 1994) studies support the effect of satiation on sharing. However, an empirical study manipulating satiation level of the beggar found no increase in begging or sharing with hungry beggars (Nissen & Crawford 1936).

Blurton Jones' model only considered what happens in the presence of an asymmetry in satiation between the players. The tolerated theft model does not explain sharing that occurs when both players are equally hungry. Harassment can influence sharing in the presence or absence of a satiation asymmetry. Wrangham (1975) first emphasized the importance of harassment (or 'sharing under pressure') when studying the Gombe chimpanzees. He suggested that a food possessor 'may use the parts that he does not need to reduce the costs of possession by "paying" other individuals to go away' (page 4.57). Moore (1984) proposed that this threat of attack from a beggar may be very costly for an owner and offered a graphical model of how costs of harassment (both physical and social) can influence sharing. Stevens & Stephens (2002) used game theory to formalize the first mathematical model of the effects of harassment on sharing. They predicted that the defensibility of a food source may influence harassment by beggars; if beggars can obtain scraps, harassment may be worthwhile; if beggars harass intensely enough, they may inflict such costs on owners that sharing becomes the best strategy (manipulative mutualism).

To demonstrate the viability of harassment as an explanation of food sharing, two predictions must hold: (1) harassment must be costly to the owner and (2) increasing harassment should increase the probability of the beggar accessing food. Harassment can include extending a hand towards an owner, vocalizing, slapping the ground, grabbing at food, or attacking the owner (Nissen & Crawford 1936; Schessler & Nash 1977; Goodall 1986; Perry & Rose 1994; Westergaard et al. 1998), possibly injuring the owner or forcing the owner to expend energy by retaliating or moving away (Wrangham 1975; Fragaszy & Mason 1983; Goodall 1986). Harassment may also impose opportunity costs associated with a reduced intake rate and the potential to lose all of the resource to the beggars. Hauser (1992) revealed that rhesus macaques, *Macaca mulatta*, that give recruitment calls experience less aggression and consume more food than those that do not recruit. Therefore, the harassment associated with not recruiting is more costly (in terms of food consumed) than the food shared after recruiting.

For food sharing to occur, the costs of harassment to the owner must outweigh the potential benefit lost by sharing (Stevens & Stephens 2002); therefore, more intense harassment should elicit more sharing. Many observational studies suggest that begging more intensely increases sharing (Nissen & Crawford 1936; Teleki 1973; Wrangham 1975; Kuroda 1984; Takahata et al. 1984; Boesch & Boesch 1989; I. C. Gilby, unpublished data) and more beggars elicit more sharing (Fruth & Hohmann 2002). In addition, an empirical study indicates that squirrel monkey, *Saimiri boliviensis*, and chimpanzee food owners share four times more often with individuals that harass than with those that do not harass (Stevens 2004).

DELAYED BENEFITS

Animals may recoup the benefits of sharing following the sharing event. This benefit can accrue after several seconds or potentially after several months. The amount of time between sharing and recouping the benefit plays an important role in the evolution of sharing, especially in short-lived animals. The bias towards primates presented here reflects the status of the literature for delayed-benefit hypotheses of sharing.

Food for Food

Reciprocity

One of the more popular explanations of food sharing is reciprocal altruism (or reciprocity), which states that an animal may perform a costly act that benefits another if the recipient returns the favour later (Trivers 1971). Computer models suggest that reciprocity is evolutionarily stable (Axelrod & Hamilton 1981), but it proves challenging to test directly, chiefly because of the difficulty in measuring the costs and benefits to fitness (Seyfarth & Cheney 1988). Relatively few studies test reciprocal altruism in a food-sharing context, and most fail to establish its importance in sharing. Some demonstrate a reciprocal sharing pattern, but do not consider that such patterns can emerge as by-products of other mechanisms. For instance, if two individuals demonstrate symmetrical attraction or aversion to each other, and such positive or negative association affects food-sharing behaviour, then a reciprocal distribution of sharing will result, even though reciprocal altruism does not explain why they share food (de Waal & Luttrell 1988; de Waal 2000; Brosnan & de Waal 2002). As an example, consider a pair of unrelated male chimpanzees that are inseparable. When potential food-sharing situations arise, both members of the pair tend to share because the other harasses. Because these two individuals spend more time with each other than with other individuals, their mutualistic sharing will appear reciprocal. This 'symmetry-based' reciprocity may explain food sharing in wild chimpanzees (Mitani & Watts 1999, 2001; Watts & Mitani 2002), vampire bats (Wilkinson 1984; Denault & McFarlane 1995) and captive tufted capuchins, *Cebus apella* (de Waal et al. 1993; de Waal 1997b). Although symmetry-based reciprocity implies reciprocal sharing, it does not necessarily involve precise accounting of costs and benefits required in traditional or 'calculated' reciprocity.

Other examples of reciprocal sharing adjust for symmetry-based reciprocity. For instance, in one study, captive chimpanzees showed a reciprocal sharing pattern, even after statistically adjusting for association patterns (de Waal 1989). Nevertheless, this correlational study identified long-term reciprocal relationships (over all trials, A tended to share with B and vice versa), but did not manipulate ownership and assess the effects of sharing in the next trial. In an experiment with captive capuchins, de Waal (2000) found that if individual A shared frequently with individual B in one particular trial, then B tended to share frequently with A in the next trial. de Waal concluded that the events of the first stage 'set the

tone' for the second; if A was nice, then B would be nice too. Unlike traditional reciprocity, such 'attitudinal reciprocity' does not require 'strict contingency between given and received services' and therefore proves less cognitively demanding (de Waal 2000, page 260). The general relevance of attitudinal reciprocity remains unclear. No studies have convincingly documented calculated reciprocity.

Negative reciprocity. Another variation on reciprocal altruism is 'negative reciprocity' or punishment. In this case, an animal punishes by inflicting a fitness cost on a defecting (noncooperative) opponent, discouraging future defection (Boyd & Richerson 1992; Clutton-Brock & Parker 1995a). Punishment differs from harassment because punishment involves delayed rather than immediate benefits. Benefits accrue in future interactions when opponents learn the contingencies of punishment and switch to cooperation. Although common in contexts such as mate guarding (Clutton-Brock & Parker 1995b), the effect of aggression on future food sharing is not well studied in nonhuman animals.

Food for Nonfood Benefits

Trade

Strict reciprocal altruism, as discussed above, assumes that reciprocation occurs in the same fitness currency as the original act. The trade hypothesis also assumes reciprocal exchange, but reciprocation occurs in a different currency (Noë & Hammerstein 1994, 1995; Noë et al. 2001). For example, players may exchange food for social favours such as grooming or support in a dominance conflict. As with reciprocity, this concept proves challenging to test directly because of the difficulty in measuring the relative fitness value of different currencies. Is grooming actually costly to perform? However, a few studies indicate that trade may elicit food-sharing behaviour for some species.

Blood sharing among vampire bats may depend on grooming. Wilkinson (1986) found that grooming frequency correlates positively with blood-sharing frequency. However, grooming may also allow the bats to assess whether an individual has recently fed, to determine the likelihood of receiving a regurgitated meal (Wilkinson 1986).

Studies of captive monkeys show that some species may trade food for other currencies. In one experiment with captive tufted capuchins, subjects in one group transferred stones to subjects in a second group, who used the stones as tools to access food (Westergaard & Suomi 1997). Subjects in the second group then transferred food to subjects in the first group. Despite the appearance of trading tools for food, food transfer occurred at a similar rate whether or not tools were needed, indicating that trade did not explain sharing. de Waal & Berger (2000) demonstrated trade in captive capuchins, suggesting that food owners that received help in a cooperative task tended to share food more frequently. In a study with captive spider monkeys, *Ateles geoffroyi*, the frequency of

dyadic grooming correlated positively with cofeeding at a monopolizable feeder, suggesting that grooming influenced tolerance at the feeding site (Pastor-Nieto 2001).

In a study with captive chimpanzees, food possessors tolerated frequent grooming partners more often, allowing them to passively acquire food (Koyama & Dunbar 1996). In another study, individual A shared more frequently with B if B had groomed A earlier in the day, but not after A had groomed B (de Waal 1989, 1997a). After food-sharing trials, possessors groomed individuals with whom they had shared less frequently than those with whom they had not shared (de Waal 1997a). This supplies the strongest evidence that chimpanzees may trade food for grooming, because the temporal pattern of taking turns exchanging grooming and food prevents one individual from gaining all of the benefits (de Waal 1989).

Some studies of wild chimpanzees also support the idea of trade. Nishida et al. (1992) showed that the frequency with which chimpanzees obtain meat from the alpha male correlates positively with the total amount of time they spend grooming with the alpha. Additionally, the alpha male tends to support those males with whom he has frequently shared meat during their dominance conflicts with other males. The authors concluded that chimpanzees use meat sharing to maintain coalitions, with the alpha male effectively trading meat for grooming and dominance support. While suggestive, this study does not rule out symmetry-based reciprocity, because an index of proximity correlated positively with the frequency with which individuals obtained meat from the alpha male.

Others also argue that chimpanzees use meat as a social or political tool to build coalitionary support (Mitani & Watts 2001) and to 'reward allies and snub rivals' (Stanford 1998, 1999). Several researchers have suggested that chimpanzees hunt to provide highly prized items to trade (Stanford et al. 1994; Mitani & Watts 2001). These authors, however, have provided no data concerning the opportunity to receive meat. Perhaps only grooming partners or allies attempt to get meat from a possessor, and possessors share meat because of other mechanisms, such as harassment.

Show-off/status enhancement

Food sharing may serve as a costly display that advertises an animal's social status. For example, meat is energetically costly and risky for chimpanzees to acquire (Boesch 1994), so sharing with others may advertise an individual's strength and health. Such a signal may intimidate rivals or attract mates. When seen begging, an individual appears weak, in essence giving up a unit of social status for a nutritional benefit (Moore 1984). Also, simply possessing a desirable food item may draw positive attention to an individual (Teleki 1973; Rijksen 1978), thus raising its social status.

As with the other cognitively complex hypotheses, the status enhancement hypothesis proves difficult to test. Proper assessment of the status enhancement hypothesis requires a long-term study that tracks both an individual's changes in social status and sharing patterns (de Waal 1989). Apart from anecdotes (Boesch & Boesch 1989),

little evidence supports meat sharing to enhance status in chimpanzees (de Waal 1989); however, some support comes from work with Arabian babblers, *Turdoides squamiceps*. These birds maintain a strict dominance hierarchy, in which dominant individuals feed insects to subordinates. Adults appear to compete to feed each other, and interfere when subordinates try to feed others (Zahavi 1990). When fed by a subordinate, a dominant male usually responds with aggression. Typically, the alpha male seeks out and feeds the beta male. Zahavi interpreted this sharing as a display, and the acceptance of food decreases the social status of the recipient.

Group augmentation

The cooperative breeding literature first introduced the concept of group augmentation (Woolfenden & Fitzpatrick 1978; Brown 1980; Wiley & Rabenold 1984; Brown 1987), although Kropotkin (1908) and Trivers (1971) alluded to these ideas earlier. By aiding unrelated individuals, a helper increases the group size, which may provide some future benefit (e.g. group territory defence in lions: Grinnell et al. 1995; Heinsohn & Packer 1995). Because the cooperator gains future benefits, this type of delayed mutualism resists cheaters; cheaters have smaller group sizes and therefore reduced future fitness (Kokko et al. 2001; Packer et al. 2001; Clutton-Brock 2002).

Lima (1989) modelled a similar situation of this 'mutual dependence' in which an individual's fitness depends on the presence of another group member, which in turn, depends on the actions of the individual. If an individual defects in an iterated Prisoner's Dilemma, its partner will probably not survive to the next round. If the probability of finding another partner is low, the defector could face a much higher predation risk as a singleton. Therefore, by cooperating, an individual increases its group size and reduces the future risk of predation.

Most examples of group augmentation still come from the cooperative breeding literature (reviewed in Clutton-Brock 2002). Although helping in cooperative breeders frequently involves group territory defence, predator vigilance and babysitting, offspring provisioning plays a large role. Often the helpers are closely related to the offspring but not always (Stacey & Koenig 1990; Cockburn 1998). Because of the frequency of helping unrelated offspring in meerkats, *Suricata suricatta*, Clutton-Brock and colleagues proposed group augmentation as a possible explanation for such cooperativeness. Helping increases pup growth and survival, thereby increasing group size (Clutton-Brock et al. 2001). Large group sizes offer direct benefits to helpers such as lower predation risk (Clutton-Brock et al. 1999) and a pool of potential helpers when the current helpers begin to breed (Brotherton et al. 2001). A similar increase in offspring number and adult survival associated with larger group size occurs in dwarf mongooses, *Helogale parvula* (Rood 1990).

Wilkinson (1992) suggested that communal nursing in evening bats, *Nycticeius humeralis*, may increase colony size and reduce predation risk. However, this 'milk dumping' could also have the immediate effect of reducing weight and decreasing energetic costs for foraging

(Roulin 2002). Extreme forms of group augmentation may include adopting or even kidnapping (and therefore provisioning) unrelated offspring to increase their group size (Woolfenden & Fitzpatrick 1984; Zahavi 1990; Heinsohn 1991), possibly to ensure the presence of helpers when they breed (Connor & Curry 1995).

DISCUSSION

This framework implies the important theoretical point that all of these explanations are not equally likely among animal species. The nature of delayed and exchanged benefits requires specialized adaptations, limiting the number of species that can reap these types of benefits.

Limitations of Hypotheses

The framework presented here indicates that a complete study of food sharing requires synthesizing the current functional explanations with potential cognitive mechanisms. Therefore, evaluating the underlying psychological constraints on animals can provide important insights into the applicability of certain hypotheses. Given that not all hypotheses will apply to all species, we can consider specific limitations for each hypothesis.

Increased foraging, predation avoidance and group augmentation

All three of these hypotheses share the following result: sharing food increases group size, which in turn, increases individual fitness. The benefits of membership in a group have been well documented (Bertram 1978; Rubenstein 1982; Packer & Ruttan 1988; Krause & Ruxton 2002); therefore, sharing to increase group size can be quite common among group-living species. We should not, however, expect these hypotheses to explain sharing in solitary or pair-bonded species. In addition, these types of sharing may be limited to large, shareable resources (Hauser & Wrangham 1987; Hauser et al. 1993). Elgar's (1986) study emphasizes this point by showing that house sparrows recruit others to a divisible/shareable pile of bread crumbs more often than to a solid/nonshareable piece of bread equivalent in mass. These rather minor restrictions indicate that the 'increase group size' hypotheses could explain many instances of sharing, but chiefly in social, cooperatively breeding, or predatory birds and mammals.

Mate provisioning

The distinction between precopulatory and postcopulatory mate provisioning is an important one. Precopulatory provisioning probably occurs most often in species with strong intersexual selection; females can then use the provisioned food as a signal of the male's fitness. Provisioning following copulation benefits monogamous species in which parental investment is crucial. Therefore, mate provisioning could be quite common given the benefit to both promiscuous and monogamous species. Nevertheless, it has been described mostly in insects, birds, cooperatively breeding mammals (Mech et al. 1999), and chimpanzees.

Harassment

Harassment has very few constraints. Two complete strangers can find themselves in a situation in which harassment can elicit sharing. Simple instrumental learning of aversive stimuli (Thorndike 1911; Skinner 1938) can condition animals to avoid harassment. How widespread is harassment? Primates have been the focus of most sharing studies, and harassment appears to be ubiquitous among them, occurring in titi monkeys, squirrel monkeys, capuchins, macaques, gibbons, bonobos and chimpanzees. Harassment also occurs in several bird species (Amat 2000) but is often referred to as 'scrounging' (Barnard & Sibly 1981; Giraldeau & Caraco 2000; Ha et al. 2003). Harassment and begging are almost universal across taxa that feed altricial offspring (reviewed in Kilner & Johnstone 1997). Extreme forms of harassment such as kleptoparasitism or food stealing may extend beyond sharing, but they are very common types of food interactions (Brockmann & Barnard 1979; Furness 1987; Durant 2000).

Reciprocity and trade

Timing of benefits could limit reciprocity and trade as general explanations of cooperation because discounting can devalue future reciprocated acts (May 1981). Studies on humans and nonhuman animals verify the effect of discounting on cooperation (Green et al. 1995; Baker & Rachlin 2002; Harris & Madden 2002; Stephens et al. 2002). Trivers (1971) emphasized the importance of timing in his original model:

The time lag is the crucial factor, for it means that only under highly specialized circumstances can the altruist be reasonably guaranteed that the causal chain he initiates with his altruistic act will eventually return to him and confer, directly or indirectly, its benefit (Trivers 1971, page 39).

Reciprocity theory must account for discounting of future benefits. In addition to requiring multiple interactions and individual recognition, reciprocity requires a low discounting rate and complex cognitive skills to track debts owed and favours given. In addition, trade requires the ability to exchange between two or more fitness currencies. How animals value and compare different types of benefits is poorly understood. Humans and some other species of primates may possess the skills necessary to reciprocate and trade (Kaplan & Hill 1985; Winterhalder 1996a; Bliege Bird & Bird 1997; Brosnan & de Waal 2002; Hauser et al. 2003), but these explanations probably do not account for cooperative behaviour in most nonhuman animals.

Status enhancement

The status enhancement hypothesis suffers from the previously mentioned problems of deferred benefits. The cumulative nature of increasing status requires a delay before benefits are realized. This should involve discounting of the sharer's return benefit, as well as memory constraints for other group members (status is, after all, relative to others). However, other types of investment in status (such as ritualized displays or contests) also delay

the return benefit and are quite common. It appears as though some animals use specialized techniques to assess status (Cheney & Seyfarth 1990), so the delayed benefits are not discounted heavily. Despite the ubiquity of dominance hierarchies and other status-assessing mechanisms, evidence of using food sharing to raise status is restricted to only a few species such as babblers, ravens (Heinrich & Marzluff 1991) and chimpanzees.

Future Directions

Historically, research on sharing and cooperation has primarily focused on explanations involving delayed benefits. In particular, many theoretical studies have investigated the role of reciprocity in the evolution of cooperation (reviewed in Dugatkin 1997); however, aside from the examples reviewed here, little empirical support exists for reciprocity in nonhuman animals (Noë 1990; Connor 1995; Pusey & Packer 1997; Stephens et al. 1997). We feel that more focus should be placed on simpler but previously overlooked explanations such as by-product mutualism, harassment and group augmentation. These hypotheses can by no means explain all instances of sharing, but their simplicity permits application to a broad range of taxa and demands their elimination before invoking more elaborate hypotheses.

Of course, multiple types of benefits can (and probably often do) occur simultaneously to shape sharing behaviour. For example, blood sharing in vampire bats could be an interaction between kin selection, reciprocity and trade (Wilkinson 1984, 1986; Denault & McFarlane 1995). In addition, simpler mechanisms could have initiated sharing, allowing the evolution of more elaborate mechanisms (e.g. food recruitment in ravens could initially have increased individual foraging efficiency but was later co-opted into a signal of status). Disentangling these interactions can provide insight into the evolution and maintenance of sharing behaviour.

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