Meat sharing among the Gombe chimpanzees: harassment and reciprocal exchange

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Sharing food with nonkin is detrimental to a food donor's fitness, unless it is matched by compensatory benefits. I evaluated two explanations for nonkin meat sharing among wild chimpanzees, *Pan troglodytes schweinfurthii*. Reciprocal exchange proposes that a possessor relinquishes food in exchange for past or future sharing or for items of a different currency (e.g. grooming, alliances or copulations). The second hypothesis is the sharing-under-pressure/harassment model, which proposes that an individual shares to avoid the costs of defending a food item against persistent beggars. At Gombe National Park, Tanzania, I collected dyadic grooming and association data during focal follows of adult male chimpanzees. I videotaped meat-eating bouts, subsequently extracting detailed begging and sharing data. There was mixed support for the reciprocal exchange hypothesis. Sharing with males was not influenced by overall association and grooming rates. Female sexual receptivity did not affect the probability of sharing, nor did sharing increase the probability of mating. Meat possessors shared larger amounts, and were more likely to share actively with frequent female grooming partners. However, this pattern may have resulted from increased harassment by these individuals. In contrast, the sharing-under-pressure hypothesis was consistently supported: the possessor's feeding rate decreased with the number of beggars, the probability of sharing increased with the occurrence and duration of harassment, and harassment decreased following sharing events. I conclude that the pattern of meat sharing among the Gombe chimpanzees is largely explained by the sharing-under-pressure hypothesis, while the significance of reciprocal exchange remains unclear.

Relinquishing all or part of a valuable, monopolizable food item seems detrimental to an individual's fitness. Nevertheless, nonkin food sharing occurs in numerous animal taxa (Stevens & Gilby 2004). A classic example is meat sharing among wild chimpanzees, *Pan troglodytes*, which occurs frequently at all long-term study sites (Mitani & Watts 2001) Chimpanzees usually hunt monkeys in groups (Stanford et al. 1994b; Mitani & Watts 2001; Gilby 2004), and it is therefore difficult for a successful hunter to avoid detection by other chimpanzees. A meat possessor often attempts to avoid others by travelling away from the kill site (Goodall 1986), climbing to the end of a branch to restrict access by other chimpanzees (Wrangham 1975) or chasing beggars away (Goodall 1986). Despite these efforts, several chimpanzees usually surround the possessor, begging for a portion of the carcass (Wrangham 1975; Goodall 1986). Begging behaviour includes pulling on the carcass and covering the possessor's mouth with one or both hands (Teleki 1973; Goodall 1986). The possessor frequently shares with these beggars, either passively by allowing them to obtain pieces or by actively facilitating meat transfer (Teleki 1973; Boesch & Boesch 1989).

Such behaviour is distinct from kin-based food sharing, which is often associated with offspring provisioning (Feistner & McGrew 1989). A parent that feeds its offspring typically advertises food or carries it back to the nest or den. For nestlings, begging may be an honest signal of hunger that elicits a feeding response (Godfray 1995), but it does not appear to impose costs on the parent. Such kin-based sharing is easily explained, but nonkin sharing is less well understood. Chimpanzee meat possessors often avoid or actively refuse to share with nonkin beggars, and begging often appears to be costly to possessors, who may be 'forced' to share. In this paper, I examine two hypotheses that have been proposed to explain nonkin food sharing among chimpanzees and other animals.

Reciprocal Exchange

Reciprocal altruism predicts that natural selection favours altruistic acts that benefit others, provided that the

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beneficiaries reciprocate, cognitive abilities are sufficient and cheating is constrained (Trivers 1971). The reciprocal exchange hypothesis operates on the same principle, but specifies exchange of different currencies, such as food and grooming (Noë & Hammerstein 1994, 1995). For example, a food donor might pay costs in the form of lost calories, but after a delay, might gain hygienic or social benefits of grooming. Reciprocal exchange in the context of food sharing has been supported in a few species, including vampire bats, *Desmodus rotundus* (Wilkinson 1986), capuchin monkeys, *Cebus apella* (Westergaard & Suomi 1997; de Waal 2000) and chimpanzees (Nishida et al. 1992; de Waal 1997a; Mitani & Watts 2001; Mitani 2005). One form of reciprocal exchange in chimpanzees is 'meat-for-allies', which proposes that males use meat as a social tool to facilitate the establishment and maintenance of intrasexual social bonds (Nishida et al. 1992; Stanford et al. 1994b; Mitani & Watts 2001). This hypothesis predicts that a meat possessor will be more likely to share with frequent grooming partners and/or 'associates'. Another form of reciprocal exchange is 'meat-for-sex', which suggests that males share meat with females in return for mating, either immediately (Stanford et al. 1994b; Stanford 1998) or during future sexual cycles (Tutin 1979). The immediate meat-for-sex hypothesis predicts that a possessor will be more likely to share with sexually receptive females, and that sharing will be contingent upon mating. Delayed meat-for-sex predicts preferential sharing with cycling females.

Sharing-under-pressure/Harassment

The 'sharing-under-pressure' hypothesis proposes that a meat possessor shares to avoid the costs of defending the carcass from persistent beggars (Wrangham 1975). This hypothesis assumes that begging is more than an honest signal of hunger; possessors suffer costs if they do not share. These costs may include reduced feeding efficiency, increased energy expenditure (avoiding or chasing beggars) and injury. Sharing provides a benefit whenever it reduces the level of harassment, and in turn, the costs of defence. This is similar to the 'tolerated theft' model (Isaac 1978; Blurton Jones 1984, 1987) of food sharing among humans. Tolerated theft assumes that the fitness benefit of food consumption follows a diminishing-returns function. Theoretically, a resource owner should eventually reach a point at which the costs of defence outweigh the benefits of further consumption. Unlike tolerated theft, however, the sharing-under-pressure hypothesis is not contingent upon a hunger asymmetry. The sharing-under-pressure hypothesis predicts that (1) harassment is costly to the possessor, (2) harassment elicits sharing and (3) sharing reduces harassment. Using a game-theoretical model, Stevens & Stephens (2002) predicted that if beggars harass enough, they may inflict such costs on possessors that sharing becomes the best strategy. In a controlled experiment, Stevens (2004) showed that sharing by captive chimpanzees and squirrel monkeys, *Saimiri boliviensis*, was associated with harassment.

Reciprocal exchange and sharing-under-pressure are not mutually exclusive hypotheses. Both address the ultimate causes of sharing, but they differ in when the benefits of sharing are realized (Stevens & Gilby 2004). Sharing-under-pressure results in an immediate benefit to the donor in the form of reduced harassment. The benefits of reciprocal sharing are delayed until the recipient returns the favour. In both cases, the costs and benefits of sharing are ultimately measured in terms of the possessor's fitness. In this study, I used observations of social interactions and video of meat sharing among chimpanzees, *P. t. schweinfurthii*, in Gombe National Park, Tanzania to test the sharing-under-pressure and reciprocal exchange hypotheses. The effects of harassment have not otherwise been measured in the wild, nor have they been addressed concurrently with reciprocal exchange. This is particularly important, because a reciprocal sharing pattern may emerge as the result of a 'hidden' variable (de Waal & Luttrell 1988; Stevens & Gilby 2004; Mitani 2005). For example, if frequent grooming partners tend to harass intensely, and possessors share to avoid the costs of harassment, a pattern consistent with reciprocal exchange would be observed, even though it did not explain the occurrence of sharing. The immediate benefits of sharing to avoid harassment have often been overlooked and could therefore explain certain aspects of sharing in natural populations.

METHODS

I collected data on the Kasekela chimpanzee community of Gombe National Park in 1999–2002, during the peak monkey-hunting months of August, September and October (Gilby 2004; Stanford et al. 1994a). Goodall (1986) provides a detailed description of the study site. I conducted full-day focal follows of five adult male chimpanzees: FR, FD, GB, AO and SL. Follows varied in frequency from season to season (Gilby 2004), and were biased towards large parties to increase the probability of witnessing a successful hunt. For the 1999 and 2000 field seasons, I followed FR exclusively because of his high hunting success rate (Stanford 1998). FR was the top-ranking male during all four data collection periods. I expanded data collection to include GB and FD in 2001 and added AO and SL in 2002. Unusual ranging and grouping patterns made male chimpanzees difficult to find during the final field season, and therefore, hunting was rare. As a result, sample sizes for GB, FD, AO and SL (Gilby 2004) were relatively small.

At 15-min intervals, I used instantaneous scan sampling (Altmann 1974) to record party composition and the focal chimpanzee's adult male and female nearest neighbours. As a measure of relative spatial and temporal association, I calculated nearest-neighbour frequency (Table 1), the percentage of each focal male's nearest neighbour tallies (per field season, per sex) accounted for by each adult male and female chimpanzee in the community. I noted all instances of grooming between the focal male and other adults, recording duration and partner identity. As a measure of relative grooming rates, I calculated grooming duration (Table 1), the percentage of focal follow time (per field season) that the focal male spent grooming with each adult male and female in the community.

Table 1. Explanatory variables used in analysis

Variable	Type	Description
Nearest-neighbour frequency	Continuous	Percentage of individual A's total nearest-neighbour tallies (per season, per sex) that individual B was A's nearest neighbour
Grooming duration	Continuous	Percentage of individual A's total seasonal focal follow time spent grooming with individual B
Association frequency*	Continuous	Percentage of individual A's yearly focal follow time that individual B was present in the same party
Grooming bout frequency*	Continuous	Number of grooming bouts between individuals A and B per 10 focal follow hours of A in a given year
Harassment occurrence	Categorical	Indicates whether holding or hand–mouth begging occurred during a begging bout
Harassment duration	Continuous	Percentage of meat-eating bout that harassment (holding or hand–mouth begging) occurred
Reproductive state	Categorical	Not cycling, cycling but not swollen, fully swollen

*Calculated from long-term data.

The unpredictable nature of meat possession prevented me from collecting grooming and nearest-neighbour data on all chimpanzees for which I ultimately obtained meat-eating data. I therefore did not include these bouts in primary analyses. However, FR was the meat possessor for more than half of the observed meat-eating bouts (see Results). To be sure that FR did not skew the results, I ran all analyses a second time, excluding his bouts. However, the sample size was not large enough to permit tests that included grooming duration or nearest-neighbour frequency. Therefore, for 'non-FR' analyses, I derived more general measures of grooming and association rates using long-term Gombe data, allowing me to include possessors for which I did not collect grooming or nearest-neighbour data. Since 1974, field assistants have conducted daily nest-to-nest focal follows of adult chimpanzees at Gombe. They systematically record party composition and keep a running account of the behaviour of the focal chimpanzee (Goodall 1986, pp. 597–608; Gilby 2004). From these records, I calculated association frequency, the percentage of total follow time (per focal chimpanzee, per year) that each adult male and adult female was in the same party as the focal male, and grooming bout frequency, the number of grooming bouts observed between the focal male and each adult chimpanzee per 10 focal follow hours of the focal male during a given year (Table 1).

When a hunt occurred, I suspended collection of grooming and association data and videotaped meat eating. My field assistant also used a video camera in 2001 and 2002. Whenever possible, we recorded meat eating by one of the five focal adult males from the moment he obtained a carcass to the moment he finished or relinquished control of it (a 'meat-eating bout'). If more than two of these males possessed meat, we gave priority to those with the fewest previously recorded meat-eating

bouts. If one of these five males did not possess meat, we videotaped those that did, choosing targets according to ease of visibility.

I used Noldus Observer VideoPro 3.0 (Noldus Information Technologies, Wagenigen, The Netherlands) to extract begging and sharing data from the video. I estimated the mass of the carcass at the start of each meat-eating bout, based on Stanford's (1998) estimates (infant: 0.5–2 kg; juvenile: 2–5 kg; subadult/adult: 5–10 kg). Using these categories as a starting point, I based the mass estimate for each individual carcass on sex, apparent age and completeness. I calculated the total amount of meat consumed by the possessor using the following formula: (starting kg – kg shared – kg stolen – final kg)/(possession time). I excluded all data (including possession time) from periods when visibility was obscured.

I defined a 'beggar' as any adult chimpanzee that approached within approximately 3 m of the meat possessor, and a 'begging bout' as the interval when a particular beggar was present during a meat-eating bout. If a beggar left the begging cluster and returned later, I included the second interval in the same begging bout. I recorded the start and end time of each instance of four types of 'begging event': (1) sit (sitting and staring at the carcass), (2) reach (reaching towards but not touching the carcass or possessor), (3) hold (touching the carcass or possessor) and (4) hand–mouth (placing a hand directly over the possessor's mouth). I classified hold and hand–mouth begging as harassment because they restricted the possessor's movement. For each begging bout, I recorded the occurrence and duration of harassment. I defined harassment duration as the percentage of the meat-eating bout that a beggar harassed the possessor (Table 1).

I noted each female beggar's reproductive state. I scored a female as (1) fully swollen, (2) cycling but not swollen or (3) not cycling (Table 1). I judged a female to be cycling if I observed her with a sexual swelling at least once during the 3-month field season. I also recorded all copulations that occurred during begging bouts.

I defined a 'sharing event' as when a beggar obtained a piece of meat from within arm's reach of the possessor, without any attempt by the possessor to retaliate or prevent the transfer. This agrees with other published definitions of sharing in that it is based on the possessor's reaction (Boesch & Boesch 1989; de Waal 1989, 1997a, b; Stevens 2004). If the possessor attempted to retrieve the piece or chased the beggar, I classified the event as 'stealing'. I recorded the occurrence of each sharing event, and classified it as active sharing if the possessor facilitated meat transfer (usually by relinquishing the portion in his mouth, or by handing a piece to a beggar). I assigned the amount shared to one of the following size categories: (1) 50 g, (2) 0.5 kg (50 g–1 kg), (3) 1.5 kg (1–2 kg), (4) 2.5 kg (2–3 kg), etc. When calculating total amounts shared, I multiplied the number of sharing events in each size category by the category value (e.g. 0.5 kg for category two), and summed across all categories.

Finally, I noted the occurrence of the following avoidance/retaliation behaviours by the possessor: (1) turn (turn away from the beggar), (2) hit (strike or push the beggar) and (3) chase (chase the beggar away from the carcass).

Statistical Analyses

I conducted all statistical analyses in SAS 8.1 (SAS Institute, Inc., Cary, North Carolina, U.S.A.). Unless otherwise noted, I used logistic regressions to examine the relation between independent and categorical dependent variables (e.g. the probability of sharing versus harassment duration). To control for within-sample correlation from repeated sampling of possessors and beggars, I used the possessor/beggar ID combination as a repeated measure (RM) in all analyses, using type III generalized estimating equations (GEE; Diggle et al. 2002), unless noted otherwise. This method adjusts estimated parameter variance based on sampling frequency, and does not report an R^2 value. I also used GEE with linear regressions. In some instances, I used multiple regression to control for the potentially confounding effects of correlated variables. In these cases, I began with the fully saturated model and removed interaction terms if they did not contribute significantly to the fit of the model ($\alpha = 0.05$).

RESULTS

My field assistant and I videotaped 65 meat-eating bouts by eight adult males. FR was the meat possessor for 35 of these bouts. I observed 96 begging bouts with male beggars (after excluding four bouts with maternal half-siblings), and 127 with female beggars (after excluding eight bouts with mothers and four bouts with maternal half-siblings) (Table 2). When I excluded FR's meat possessions, there were 41 bouts with male beggars and 53 bouts with female beggars across the remaining seven possessors. The majority of prey were red colobus monkeys, *Colobus badius tephrosceles*, but there were also two infant olive baboons, *Papio anubis*, two redtail monkeys, *Cercopithecus ascanius*, one young bushbuck, *Tragelaphus scriptus*, and one young bushpig, *Potomochoerus porcus*. Meat possessors consumed a mean ± SD of 1.16 kg ± 0.63 (range 0.25–2.5) per meat-eating bout, at a mean ± SD rate of 1.9 ± 1.2 kg/h (range 0.1–5.2) and faced a mean ± SD of 3.7 ± 1.9 beggars (range 1–10). In several cases, the possessor gained control of the carcass after it had been divided. The maximum amount consumed by a possessor during a single meat-eating bout was 2.5 kg. For 43 (66%) of the 65 meat-eating bouts, the amount of meat initially controlled by the possessor was 2–3 kg, an amount that could theoretically have been consumed entirely by the possessor. I found a positive correlation between carcass mass and the number of beggars (linear regression: $F_{1,56} = 26.44$, $P < 0.0001$, RM: possessor). Passive sharing occurred in 62 (95%) of the 65 meat-eating bouts and active sharing occurred in 40 (62%). Meat possessors shared a mean ± SD of 39 ± 28% (range 0–94%) of the mass that they started with.

Sharing-under-pressure/Harassment

Begging was costly to the possessor

The possessor's meat consumption rate decreased with the number of beggars per meat-eating bout (linear regression, $F_{1,56} = 5.82$, $P = 0.02$, RM: possessor; Fig. 1). This

Table 2. Number of begging bouts for each meat possessor, separated by sex of beggar

| | Number of bouts | | | |
| | Male beggars | | Female beggars | |
Possessor	Total	Social data	Total	Social data
AO	3 (3)	1 (1)	7 (6)	4 (4)
FD	3 (3)	1 (1)	4 (3)	5 (4)
FR	55 (9)	54 (9)	74 (15)	72 (15)
GB	9 (6)	6 (5)	20 (13)	16 (13)
KS	1 (1)		1 (1)	
SL	5 (4)	2 (2)	7 (7)	2 (2)
TB	18 (8)		7 (5)	
WL	2 (1)		7 (6)	
Total	96 (11)	64 (11)	127 (20)	99 (19)

Numbers in parentheses indicate the number of different beggars. Bouts without social (grooming and nearest-neighbour) data resulted from meat possession by males that were not the subject of focal follows during a given field season.

negative relationship remained significant when carcass mass was statistically controlled for using multiple regression ($F_{1,55} = 8.37$, $P = 0.005$), indicating that the decrease in consumption rate from the presence of beggars was independent of any tendency to eat large carcasses more slowly.

The probability that a possessor showed avoidance and/or retaliation behaviour (turn, hit, push or chase) during a begging event increased with the duration of the begging event (logistic regression: $\chi_1^2 = 12.56$, $P = 0.0004$, odds ratio: 1.002). This result remained when the type of begging event (sit, reach, hold, hand–mouth) was statistically controlled for using multiple regression. The probability of avoidance and/or retaliation behaviour was not associated with the type of begging event ($\chi_3^2 = 6.11$, $P = 0.11$).

Sharing was associated with harassment

Within a begging bout, the probability that sharing occurred during a specific begging event (sit, reach, hold
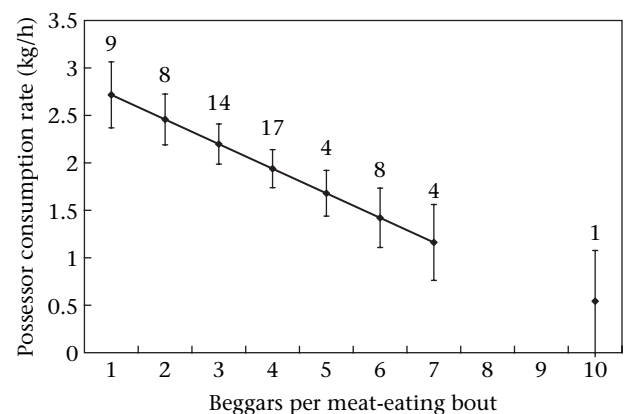

Figure 1. Marginal (repeated measure: possessor) regression line ± SE of possessor's meat consumption rate as a function of the number of beggars per meat-eating bout. Values above each point indicate sample size.

or hand–mouth) was associated with the type of begging event (male beggars: $\chi_3^2 = 11.8$, $P = 0.008$; female beggars: $\chi_3^2 = 17.5$, $P = 0.0006$; Table 3). For beggars of both sexes, sharing was more likely to occur during holding or hand–mouth begging events than during sitting events. For female beggars, sharing was also more common during reaching events than sitting events, and there was no significant difference between the probability of sharing during holding and hand–mouth events, but both were better predictors of sharing than reaching was. For male beggars, holding was the best predictor of sharing.

Active sharing was associated with begging event type for female beggars ($\chi_3^2 = 11.4$, $P = 0.009$), but not for males ($\chi_3^2 = 3.96$, $P = 0.27$). For females, active sharing followed hand–mouth begging most commonly, and holding and reaching predicted statistically similar odds of active sharing (Table 3).

Comparing entire begging bouts, the probability of sharing was significantly higher when a beggar harassed the possessor at least once during the bout (male beggars: $\chi_1^2 = 16.19$, $P < 0.0001$, odds ratio: 17.5; female beggars: $\chi_1^2 = 21.14$, $P < 0.0001$, odds ratio: 35.5). The same was true for the probability of active sharing (males: $\chi_1^2 = 8.11$, $P = 0.004$, odds ratio: 22.6; females: $\chi_1^2 = 13.56$, $P = 0.0002$, odds ratio: 22.4), and sharing at least 0.5 kg (males: $\chi_1^2 = 9.07$, $P = 0.003$, odds ratio: 5.7; females: $\chi_1^2 = 8.29$, $P = 0.004$, odds ratio: 28.8). There was also a positive association between sharing and harassment duration. The percentage of the meat-eating bout that a beggar harassed was positively associated with sharing (male beggars: $\chi_1^2 = 8.26$, $P = 0.004$, odds ratio: 2.5; female beggars: $\chi_1^2 = 8.46$, $P = 0.004$, odds ratio: 3.2), active sharing (males: $\chi_1^2 = 4.76$, $P = 0.03$, odds ratio: 1.1; females: $\chi_1^2 = 4.73$, $P = 0.03$, odds ratio: 1.1) and sharing at least 0.5 kg (males: $\chi_1^2 = 4.07$, $P = 0.05$, odds ratio: 1.1; females: $\chi_1^2 = 5.36$, $P = 0.02$, odds ratio: 1.2). The probability of sharing increased dramatically with a small increase in harassment duration (Fig. 2). If a male beggar never harassed, the probability of sharing was only 0.38 (0.27 for females). However, for beggars of either sex that harassed for at least 6% of the meat-eating bout, the probability of sharing was 1.0. In contrast, the probability of either active sharing or sharing at least 0.5 kg increased much more slowly with harassment duration. For example, a male beggar that harassed for 23% of the bout had an 86% chance of receiving at least 0.5 kg of meat and a 70% chance of receiving meat through active sharing (Fig. 2a). The pattern was the same for female beggars (Fig. 2b).

When I excluded FR from these analyses, the positive association between harassment duration and active sharing was no longer statistically significant ($\chi_1^2 = 1.05$, $P = 0.3$). Otherwise, removal of FR did not affect the association between harassment and sharing, either at the level of begging event or begging bout.

Sharing recipients ceased begging

Beggars of either sex showed higher probability of departure from the begging cluster immediately following a sharing event than they showed immediately following a begging event ($\chi_1^2 = 406$, $P < 0.0001$). Specifically, I recorded beggars as 'absent' immediately following 34% of sharing events ($N = 434$), but I recorded only 6.5% of beggars as 'absent' after a begging event ($N = 5136$; Fig. 3).

Reciprocal Exchange

Male beggars: grooming and association

In bouts with male beggars, grooming duration was not associated with the probability of sharing ($\chi_1^2 = 0.66$, $P = 0.4$), active sharing ($\chi_1^2 = 0.09$, $P = 0.8$) or sharing at least 0.5 kg ($\chi_1^2 = 0.0$, $P = 0.97$). Nearest-neighbour frequency also did not predict sharing ($\chi_1^2 = 0.0$, $P = 0.96$), active sharing ($\chi_1^2 = 2.26$, $P = 0.13$) or sharing at least 0.5 kg ($\chi_1^2 = 1.74$, $P = 0.19$). Results were identical when I removed FR from the analysis and used long-term

Table 3. The probability of sharing during begging events of different types, within begging bouts

| | Male beggars | | | Female beggars | | | | | |
| | Sharing | | | Sharing | | | Active sharing | | |
	Odds ratio	χ_1^2	P	Odds ratio	χ_1^2	P	Odds ratio	χ_1^2	P
Beg event type*									
Hold	9.4	95.1	<0.0001	17.5	210.8	<0.0001	35.2	27.6	<0.0001
Hand–mouth	6.1	29.6	<0.0001	9.87	56.4	<0.0001	164.0	42.5	<0.0001
Reach	1.0	0.01	0.91	2.69	10.56	0.001	8.8	12.5	0.0004
Sit	—	—	—	—	—	—	—	—	—
Contrast†									
Hold vs hand–mouth		6.61	0.01		3.05	0.08		4.56	0.03
Hold vs reach		9.16	0.003		6.58	0.01		2.17	0.14
Hand–mouth vs reach		4.18	0.04		4.38	0.04		4.85	0.03

The results of marginal logistic regressions of the probability of sharing during begging events of different types.
*Probability of sharing during holding, hand–mouth and reaching events compared to sitting events.
†Tests for significant differences between all begging event types in their effect on sharing (e.g. for male beggars, sharing was significantly more likely to occur during a holding event than during a hand–mouth event; $\chi_1^2 = 6.61$, $P = 0.01$).
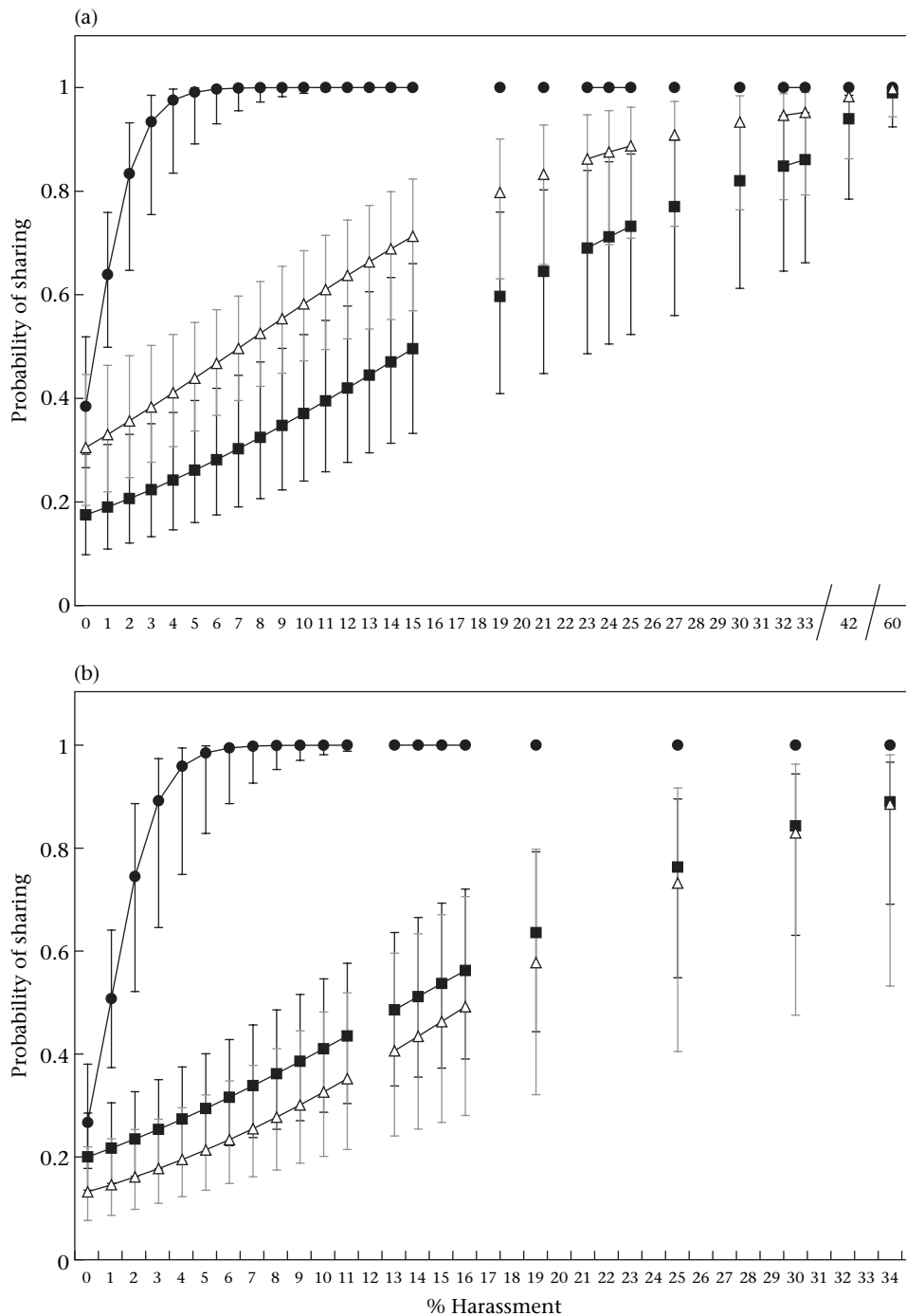
(a)

(b)

% Harassment

Figure 2. Sharing versus harassment duration across begging bouts for (a) male beggars and (b) female beggars. Marginal logistic regression lines (with 95% confidence intervals) of the probability of sharing (●), active sharing (■) and sharing at least 0.5 kg (△) as a function of harassment duration (percentage of the meat-eating bout that the beggar showed holding or hand–mouth begging).

grooming and association data to allow for inclusion of all possessors (see Methods).

Female beggars: grooming and association

In bouts with female beggars, nearest-neighbour frequency was not associated with sharing ($\chi^2_1 = 1.64$, $P = 0.2$), active sharing ($\chi^2_1 = 2.75$, $P = 0.1$) or sharing at least 0.5 kg ($\chi^2_1 = 2.71$, $P = 0.1$). There also was no

association between grooming duration and the probability of sharing ($\chi^2_1 = 1.97$, $P = 0.16$). There were positive but nonsignificant ($\alpha = 0.05$) associations between grooming and active sharing ($\chi^2_1 = 3.63$, $P = 0.06$, odds ratio: 2.5) and between grooming and the probability of sharing at least 0.5 kg ($\chi^2_1 = 3.12$, $P = 0.08$, odds ratio: 2.08). When I restricted analysis to bouts with FR as possessor, these associations were statistically significant (active sharing: $\chi^2_1 = 4.04$, $P = 0.04$, odds ratio: 1.52; large share:
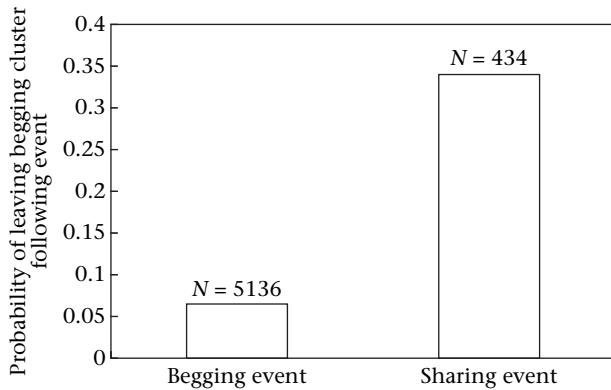
Figure 3. Probability of beggar departure following sharing versus begging events.

$\chi_1^2 = 3.76$, $P = 0.05$, odds ratio: 1.97). However, when statistically controlling for the duration of harassment using multiple regression, these associations were no longer statistically significant (active sharing: $\chi_1^2 = 0.1$, $P = 0.75$; ≥ 0.5 kg; large share: $\chi_1^2 = 1.29$, $P = 0.25$). This result suggests that frequent female grooming partners may beg more persistently, which leads, in turn, to more sharing. The duration of harassment by female beggars (in bouts with FR) was positively associated with grooming duration (generalized linear mixed model: $F_{1,56} = 32.13$, $P < 0.0001$; Fig. 4).

Female beggars: reproductive state and mating

There was no statistically significant association between reproductive state (noncycling, cycling but not swollen, swollen) and sharing (sharing: $\chi_2^2 = 1.78$, $P = 0.4$; active sharing: $\chi_2^2 = 1.07$, $P = 0.6$; ≥ 0.5 kg: $\chi_2^2 = 2.14$, $P = 0.3$), even after removing FR from the analysis. Results were the same if I categorized reproductive state by swelling state only (yes or no).
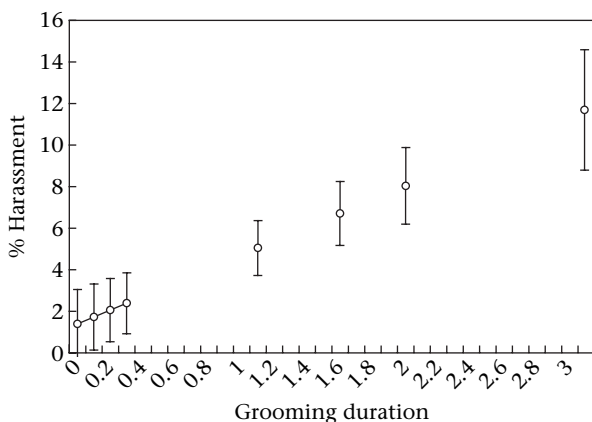

Figure 4. Harassment duration versus grooming duration for females begging from the top-ranking male, FR, showing the regression line from a generalized linear mixed model of harassment duration (percentage of meat-eating bout in which a beggar harassed) as a function of grooming duration (percentage of FR's total grooming time). Error bars show 95% confidence intervals.

Mating occurred in 28% (10/36) of begging bouts with swollen females, and it occurred more often during bouts in which sharing occurred (35% of 23 bouts) than during nonsharing bouts (15% of 13 bouts), but this difference was nonsignificant ($\chi_1^2 = 1.62$, $P = 0.2$, marginal logistic regression, repeated measure: possessor/beggar). The lack of statistical significance was probably partly because of repeated sampling of male–female dyads. Five dyads accounted for 23 of the 36 bouts. After removing the effects of these correlated data, there was no evidence that sharing increased the likelihood of mating.

DISCUSSION

Sharing-under-pressure/Harassment

The results support the sharing-under-pressure/harassment model of food sharing. Consistent with the first prediction of the hypothesis, begging imposed costs on the possessor. First, as the number of beggars increased, a possessor consumed meat more slowly, presumably at the expense of other activities. However, the degree to which the fitness benefits of meat eating correlate with feeding efficiency is unknown. It is possible that the total amount consumed may be more important than rate at which it is eaten. Nevertheless, begging also imposed energetic costs. The possessor was more likely to turn away from, hit and/or chase a beggar during long begging events than during short begging events, thus expending energy in response to beggar behaviour. Retaliation and avoidance, however, were not associated with the type of begging event. However, other factors, such as the behaviour of other beggars or the sequence of begging event types, may contribute to the magnitude of a possessor's response.

That begging imposes costs on the possessor is a critical component of the sharing-under-pressure hypothesis, because it demonstrates an incentive to share. I found a strong relationship between sharing and harassment. Within a begging bout, sharing was more likely to occur during harassment events (holding or hand–mouth begging) than during sitting or reaching events. Male beggars were most likely to receive meat when they were holding onto the carcass. Female beggars were equally likely to be successful during holding and hand–mouth begging events, but were most likely to receive meat through active sharing when they were begging hand-to-mouth. These results indicate that possessors reacted to begging behaviours that restricted their movement (and presumably their feeding efficiency). However, possessors did not always respond immediately to harassment events by sharing. Specifically, active sharing with male beggars occurred independently of begging event type, perhaps because possessors also base sharing decisions upon other factors, such as cumulative harassment. Indeed, for beggars of both sexes, sharing was positively associated with total harassment duration. If a beggar harassed for only a small percentage of the bout, then s/he was very likely to get a small amount of meat. However, as harassment duration increased, the possessor was more likely to share actively and to share larger amounts.

There was some evidence that possessors responded differently to harassment. When possessions by the alpha male were removed from the analysis, active sharing was no longer associated with harassment duration (although it was still associated with harassment occurrence). It is unclear whether this result represents a true difference or instead was caused by small sample size. However, it would be surprising if the alpha male responded more to harassment than did other males, because he outranks all beggars. Perhaps he gave up meat more readily than did other possessors because he consumed meat relatively frequently.

The observation that sharing reduced the begging pressure on a meat possessor provides a third line of evidence supporting the sharing-under-pressure hypothesis. Beggars were more likely to leave the begging cluster immediately following a sharing event than following a begging event. The negative relationship between the number of beggars and consumption rate means that reducing the number of beggars increases the possessor's meat consumption rate. By sharing, a possessor increased the probability that a beggar moved away, thereby increasing his own feeding efficiency. This is the first study to show such an immediate benefit of sharing, a key requirement of the sharing-under-pressure hypothesis.

Harassment appears to be a key factor in obtaining meat, so why is there such variation in harassment intensity between beggars? Why is harassment not ubiquitous? Differences in harassment rates are likely to result from individual variation in the benefits and costs of begging. The nutritional benefits may be greater for pregnant or lactating females, who may have a greater need for protein- and fat-rich foods than do cycling females. Therefore, we might expect such females to beg more persistently. However, earlier analyses showed that a female's begging persistence was not associated with her reproductive state (Gilby 2004). The magnitude of the benefit may also vary with age and recent diet. Old individuals, or those with recent dietary deficiencies, may enjoy disproportionately high benefits from a scrap of meat and may therefore be more likely to harass a possessor for a share. In this study, the two oldest males in the community (GB and BE) were extremely persistent (and successful) in their efforts to obtain meat. This may explain why older males in other chimpanzee populations are more likely to receive meat than younger males (Nishida et al. 1992; Boesch 1994). The costs of harassment to the beggar may include increased aggression and wasted time and/or energy (Wrangham 1975). Begging could also impose a social cost, because it may serve as an acknowledgment of lower status (Moore 1984), predicting a negative association between rank and harassment intensity.

The importance of harassment in other chimpanzee populations remains to be studied in detail. There is no obvious reason to believe that the costs and benefits of begging differ considerably between populations. Many accounts of sharing among chimpanzees indicate that harassment is a critical component of sharing (Nissen & Crawford 1936; Teleki 1973; Wrangham 1975; Kuroda 1984; Boesch & Boesch 1989; Stevens 2004). There is also evidence of an association between harassment and sharing in other species. Captive squirrel monkeys share four times more often with individuals that harass than with those that do not harass (Stevens 2004). Rhesus macaques, *Macaca mulatta*, that do not recruit others to a valuable food source experience more aggression and consume less food than do those that share (Hauser 1992). Harassment may also explain sharing in species without the cognitive abilities required for reciprocal exchange.

Reciprocal Exchange

I found mixed support for the reciprocal exchange hypothesis. Meat possessors were more likely to share actively and to share large amounts with female beggars with which they frequently groomed. However, this relationship was statistically significant only when restricted to possessions by the alpha male. This result suggests that individual chimpanzees have different sharing strategies. Perhaps some share in return for past favours but others do not. Nevertheless, this is the first evidence from a wild population that a male's relationship with a female may affect his tendency to share meat with her. Previous studies of males sharing meat with females have focused almost exclusively upon meat for sex (see below).

In contrast, there was no evidence of preferential sharing with frequent male grooming partners or nearest neighbours. Unfortunately, sample size and data collection protocol prevented the use of the matrix correlation techniques (Hemelrijk 1990) that are commonly used to test for reciprocal exchange in chimpanzees (de Waal 1989; Mitani et al. 2000; Mitani & Watts 2001; Mitani 2005) and other animals (Hemelrijk 1994). However, the method that I used uncovered evidence of reciprocal exchange with females, so it is interesting that there was no such trend for males. This result is particularly important in light of assertions that meat sharing is critical in establishing and maintaining long-term cooperative relationships between male chimpanzees. Why does this not appear to be the case at Gombe? One hypothesis is that males at different sites differ in their tendency to cooperate. Ngogo is an unusually large community, with more than 25 adult males (Mitani & Watts 1999; Mitani 2005), compared to 12 at Gombe. Males at Ngogo undoubtedly experience more intense competition for dominance and may therefore be more likely than Gombe males to form long-term cooperative alliances. Ngogo males may therefore use meat as a 'commodity' to trade for grooming and/or coalitionary support. At Ngogo, males reciprocated grooming, coalition formation and meat sharing (Mitani 2005). However, this argument does not explain why the alpha male of a nine-adult-male community in Mahale Mountains National Park, Tanzania, shared preferentially with frequent coalition partners (Nishida et al. 1992). I was unable to test whether Gombe males exchanged meat for coalitionary support, but this was unlikely, because support has been shown to be correlated with grooming and association rates (Mitani et al. 2000).

The results from the present study add to the growing body of literature on reciprocal exchange of different currencies (reviewed in Mitani 2005). Few studies have addressed such exchange in a food-sharing context. Work by de Waal is a notable exception. At the Yerkes Primate Center, female chimpanzees are more likely to share bundles of plant material with others after being groomed by them (de Waal 1989, 1997a), showing that chimpanzees have the cognitive ability for reciprocal exchange. The strongest evidence for reciprocal exchange of food with other commodities in the wild comes from Ngogo, where rates of meat sharing, grooming and coalitionary support are correlated among males (Mitani & Watts 2001; Mitani 2005).

Reciprocal Harassment

A sharing pattern that is consistent with reciprocal exchange might emerge as the by-product of another mechanism. For example, if two individuals of a similar age/rank class demonstrate symmetrical attraction to each other, and such association affects sharing, a reciprocal sharing pattern would emerge (de Waal & Luttrell 1988; de Waal 2000; Brosnan & de Waal 2002). Many food-sharing studies control for such 'symmetry-based' sharing, and still find a reciprocal sharing pattern (e.g. de Waal 1989; Mitani 2005). Harassment is another mechanism that may contribute to a pattern of sharing consistent with reciprocal exchange. For example, if individual A grooms individual B, then A may be more likely to harass when B possesses meat. For A, the earlier grooming might lower the costs of harassment by increasing B's tolerance of A's begging. If B shares in response to A's harassment, a pattern consistent with reciprocal exchange would emerge, even though reciprocal exchange did not explain why sharing occurred. Results from the present study are consistent with this idea. Females with which the alpha male frequently groomed were more likely to show harassment behaviour than other females were. When I statistically controlled for harassment duration, there was no longer any evidence for preferential sharing with these females. At a given level of harassment, grooming rates did not influence the probability of active sharing or of sharing large amounts.

While harassment certainly cannot account for all sharing, these results on natural sharing behaviour confirm experimental findings (Stevens 2004) in demonstrating that harassment can account for some instances of sharing. The costs of possession, therefore, must be considered in order to gain a more complete picture of why chimpanzees and other species share food. For example, in Taï National Park, Côte d'Ivoire, male chimpanzees share meat preferentially with individuals that join in cooperative hunts (Boesch 1994; Boesch & Boesch-Achermann 2000). Perhaps unsuccessful hunters beg more persistently than nonhunters, because they have a stronger desire for meat.

Meat for Sex

This study did not support the meat-for-sex hypothesis. First, there was no evidence of preferential sharing with maximally swollen females. At Gombe, 96% of copulations are with maximally swollen females (Goodall 1986), so if meat was being exchanged for an immediate mating, one would expect to observe elevated rates of sharing with swollen females. Second, there was no preferential sharing with cycling females, indicating that the potential for future mating did not serve as an added incentive to share. Third, mating was equally likely to occur during sharing and nonsharing bouts, indicating that sharing did not increase the probability of mating.

These results are consistent with recent studies of chimpanzees from other sites. At Ngogo, sharing did not increase the likelihood of copulating with particular females (Mitani & Watts 2001; Watts & Mitani 2002). Similarly, in captivity, sharing was not correlated with the probability of copulating (Hemelrijk et al. 1992) or siring offspring with a particular female (Hemelrijk et al. 1999).

Conclusions

Explanations for nonkin food sharing that involve immediate benefits to the food donor are often overlooked. The results of this study show that male chimpanzees at Gombe chose to share rather than suffer costs imposed by persistent beggars. Previous studies of food sharing (and many other nonhuman primate behaviours) have tended to invoke reciprocal exchange to explain food sharing. However, I found no evidence that male chimpanzees at Gombe swap meat for grooming or social allegiance. Grooming rates influenced sharing with female beggars, but this appears to have been the result of increased harassment by frequent grooming partners. There was no evidence that males trade meat for sex.

Both reciprocal exchange and harassment (tolerated theft) have been proposed to explain food sharing among human hunter-gatherers (Winterhalder 1996; Gurven 2004). Research on the Meriam (Bliege Bird & Bird 1997) and the Hadza (Hawkes 1993, 2000) supports tolerated scrounging. In contrast, a recent review of the behavioural ecology of human food sharing (Gurven 2004) argues that human food sharing is best explained by reciprocal altruism, downplaying the importance of tolerated theft. Studies of sharing among nonhuman animals, particularly chimpanzees, which anthropologists often use as models of early hominids, provide valuable insight into the origins of sharing in humans.

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