5. FOOD SHARING AND STATUS IN UNPROVISIONED BONOBOS

Gottfried Hohmann & Barbara Fruth

Sharing of food has been reported from different primate species, including marmosets (Goldizen 1986), douc langurs (Kavanagh 1972), gibbons (Schessler and Nash 1977), chimpanzees (Lavick-Goodall 1968; Nishida 1970; McGrew this volume), bonobos (Kuroda 1984; Badrian and Malenky 1984), and in the vast literature on the topic in humans (see Kaplan 1983 for a comprehensive review). Attempts to explain the evolution and manifestation of food sharing have involved various mechanisms, including kin selection (Axelrod and Hamilton 1981), reciprocal altruism (Trivers 1971), contest over resources (Blurton Jones 1984), and selfish behavior (Moore 1984). The benefits of food sharing among close kin (e.g. mother/offspring) are obvious and do not require reciprocation. In case of food sharing among unrelated individuals, however, sharing is thought to become beneficial for the donor if the recipient reciprocates food sharing at another time and/or with another "currency" (e.g. grooming, defense, mating opportunities) or if begging for food raises the social status of the donor (de Waal 1989; Strum 1975). Sharing with distantly related individuals thus can be part of strategies to rise in status via alliance formation or food distribution, among other things. Since the status structure of bonobos groups is not yet well understood, in this chapter we will give the results of our study on food sharing, and then present a hypothesis concerning food sharing and status: that food sharing is one means of forming and maintaining alliances among females, and that it is partly through such alliances that females maintain higher status than males.

The most common mode of food sharing among primates is that observed between mother and offspring (Eibl-Eibesfeldt 1971). It involves mostly plant foods and is thought to promote independent foraging and feeding by infants (McGrew 1975; Silk 1978). By contrast, food sharing between mature individuals seems to involve predominantly animal prey (Teleki 1973; Nishida 1970) or provisioned plant foods like bananas and sugar cane (McGrew 1975; Kuroda 1984).

Reports on hunting and meat sharing are derived almost exclusively from field studies on chimpanzees (e.g. Goodall 1963; Kawabe 1966; Boesch and Boesch 1989); it is widely assumed that collective hunting and subsequent division of meat were pacemakers in human evolution (Thompson 1976; Isaak 1978). It is further understood that hunting and meat sharing are behavioral predispositions, facilitating the development and manifestation of a division of labor (McGrew 1992).

Detailed analyses of the sharing of plant foods have been made from studies of chimpanzees from Gombe (McGrew 1975) and bonobos at Wamba (Kuroda 1984). In both studies, habituated individuals were regularly provisioned with bananas (Gombe) or sugar cane (Wamba) at specific feeding sites. Although the same authors also have reported on the exchange of natural plant foods, analyses focused predominantly on data collected at the respective feeding sites. In the case of Gombe chimpanzees, sharing occurred most frequently (86 percent) between mother and offspring and only infrequently (10 percent) between male and unrelated female (McGrew 1975). This is in contrast to bonobos, where sharing between males and unrelated females exceeded the rates of all other possible dyads (Kuroda 1984; Kano 1992).

Considering the thousands of hours of observation on feeding behavior of chimpanzees collected during the last decades, it has become evident that in most populations division of natural plant foods may, indeed, be of restricted significance. One exception is the chimpanzees at Tai forest, whose sharing of natural plant food (e.g. *Coula edulis, Panda oleosa*) between mother and infant is habitual (Boesch and Boesch 1984). Compared to chimpanzees, the current knowledge on sharing of natural food among mature bonobos is still fragmentary. From studies at Wamba and Lomako it is known that bonobos share various types of natural plant food (Kano 1980; Kuroda 1984; Badrian and Badrian 1984; Badrian and Malenky 1984). Hunting for meat has also been observed at both study sites (Badrian and Malenky 1984; Ihobe 1992), but meat sharing was seen only once at Lomako (Badrian and Badrian 1984).

The grouping patterns of bonobos are more or less identical to that of common chimpanzees (McGrew this volume). Communities split into temporarily stable parties of differing size and composition. Males are philopatric, whereas females leave their natal community. In contrast to chimpanzees, bonobos more often form unisexual coalitions, male bonding is comparatively weak, and dominance relationships between sexes are biased in favor of females (White 1988; Wrangham 1986; Parish 1993; author's own data). Displacements and the outcomes of agonistic interactions suggest differences in status among different community members. However, the details of the acquisition and maintainance of social rank have not yet been studied and the same applies to the genetical relationships between community members.

This chapter reports on twenty-one cases of food sharing involving meat (two cases) and natural plant foods (nineteen cases). It presents data on (1) the type of food shared, (2) the size and composition of parties during food sharing, (3) the distribution of different roles (owner, recipients) among males and females, (4) the duration and course of food sharing episodes, and (5) the behavioral interactions related to food sharing. Data from this study are then compared with previous reports from bonobos at Lomako and Wamba as well as with data from chimpanzees where males are clearly dominant.

Methods

Data on food sharing were collected between August 1990 and July 1991 and again between February and August 1992 in Lomako (Zaire). The Lomako forest is located in the Upper-Tshuapa district of Equateur in central Zaire. Detailed descriptions of the location, climate, flora, and fauna of this area have been published by Badrian and Badrian (1984), Malenky and Stiles (1991), and White (1989, 1992). All subjects involved in this study were thought to belong to the Eyengo community (which is synonymous with the term "Rangers" used by White 1988) residing in the eastern part of the Lomako study site (Badrian and Badrian 1984). From previous studies at Lomako (e.g. Badrian and Malenky 1984; White 1988, 1992; Malenky and Stiles 1991), members of this community were accustomed to the presence of human observers. However, according to White (1992), the Eyengo community was less frequently observed and less habituated than the neighboring community ("Hedons"). Perhaps for that reason observations made during the initial part of our study were limited to times when the bonobos were engaged in arboreal activities (feeding, foraging, resting). During the course of field work, subjects became more tolerant, and later it was possible to follow parties on the ground for extended periods of time. During the first part of the study (August 1990 until July 1991), twenty-two mature community members (eight males, fourteen females) could be identified using facial features and anatomical deficiencies. This figure remained stable during the second field stay. Except for two infants born in the time between the two field periods, the exact age of the subjects was not known. Therefore, estimates on the subjects' ages were based on physical criteria such as body size, development of external genitals, physiological changes (e.g. cycling), condition of teeth, and frequency of participation in specified social interactions.

Members of the Eyengo community were observed for a total of 412 hours (corrected for simultaneous observations of two observers). Duration of constant observation (visual contact with at least one individual) varied between several minutes and eleven and a half hours. Observation distance primarily depended on whether the bonobos were in trees or on the ground, and under the latter condition varied between five and fifteen meters. Whenever possible observation started at dawn, before the bonobos left the nest site occupied during the previous night. Once contact was established, it was continued for as long as possible. The data on food sharing were collected *ad libitum*. During food sharing, interindividual distances were usually very low (less than one meter), and therefore most or all individuals involved were clearly visible to the observer. In all cases except one observations were made simultaneously by two observers from different positions. Data were recorded online and simultaneously as spoken protocols using a dictaphone (Grundig-220), an audio cassett recorder (Sony Walkman) or a SVHS camcorder (Bauer-Bosch). Data on weight and size of the fruit of *Treculia africana* were collected with a portable balance and a tape measure.

Assessments of "party size" refer to counts of clusters of bonobos and include animals of all age and sex groups, except for dependent infants. Such clusters were characterized by close spatial proximity as well as coordination of general activities like rest and locomotion. Because of the restricted visibility on the ground, scores for party size were sampled either when the subjects had occupied a feeding tree or during periods of rest and/or stationary feeding on the ground. The samples used in this analysis refer only to parties encountered during day time, but do not include counts obtained from night-nest groups.

Evaluations of the "social status" were based on the outcomes of agonostic interactions. However, use of this criterion sometimes produced conflicting results, suggesting that the individual status may be strongly affected by other factors like size and composition of parties or attendance of particular individuals.

Figures on the "adult-sex-ratio" presented in the text express the relation of mature males to mature females within a given party. In the absence of any precise data on the age of the subjects, reliable separation of adults from adolescent individuals was difficult or not possible. Therefore the assessments of sex ratios include both age groups. For calculations of adult age sex ratios, the following formula used by Kano (1982) was applied:

$$\frac{\text{adult + adolescent females}}{\text{total of adult + adol. individuals}}$$

Definition of Behavioral Categories and Terminology

Sex: In addition to heterosexual matings, female bonobos display a sexual interaction known as genito-genital rubbing, where two females make contact in a ventro-ventral position and rub their genitals laterally against each other (Kuroda 1980). A specific sound may accompany this interaction.

Begging: This behavioral category includes a number of expressive movements, gestures and vocalizations previously described by Kuroda (1984), De Waal (1988), and Kano (1992). The typical facial expression is "silent pout" (De Waal 1988), the typical gesture is extending one hand close to the mouth or hand of an animal who owns food. Vocalizations like "pout moan" (De Waal 1988) and movements like body rocking may emphasize the begging.

Agonistic behavior: Agonistic interactions involve a variety of motions, facial expressions, and vocalizations (De Waal 1988). In the field, an agonistic interaction was scored when one animal tried to displace another one, independently of whether the threatening behavior involved was lunging, an arm sway or a charging display.

When two or more individuals ate simultaneously from the same piece of food a "food sharing episode" was registered. Assessments of the duration of episodes derived from the protocols recorded during field observation. The food sharing episode started with the first food exchange and was terminated when the food was completely consumed, abandoned or when it was acquired by a new owner who did not share with the former one.

The term "food sharing party" applies to all individuals present at the time of food sharing. The term "owner" was used for an individual holding part or an entire food item close to its body and/or preventing access by other individuals. "Recipients" were individuals other than the owner who ate from the same food simultaneously.

Food was never handed out by the owner but recipients always acquired food either by active taking or begging. The third category of members of food sharing parties included individuals (1) consuming food without sharing (solo feeding) simultaneously to food sharing, (2) sitting in close proximity to those sharing but not receiving any food, (3) consuming scraps of food when the shared food was abandoned, or (4) catching bits of food dropping during food consumption by another individual.

The term "transfer" is distinct from sharing and refers to a change in ownership of food from one individual (owner-1) to another (owner-2).

Results

Analyses of food sharing presented below are based on twenty-one food-sharing episodes observed and documented in detail. The majority of food sharing occured over plant foods, but two episodes involved animal prey. Figure 5.1 presents data on (1) the type of food, (2) the number and sex of bonobos involved, (3) the duration of episodes, and (4) the occurrance of food transfers. Except for one case of *Treculia*-sharing, one individual was obviously the owner, carrying and/or holding the food item divided close to its body. The single exception was a case when three mature females and one mature male collectively consumed a *Treculia* fruit.

In the two cases of meat sharing, hunting and killing of the prey were not observed, but according to the noise that was thought to accompany the capture as well as the condition of the prey at the time of discovery by the observers the delay between capture of prey and onset of observation seemed to be very short (less than five min). The first episode involved an unidentified mammal of small size (e.g. large squirrel). The only remains found after a half hour of observation at the site of meat sharing were drops of a soft, cream-colored and strong-smelling secretion. The second case involved a medium-sized duiker *(Cephalophus sp.)* with an estimated weight of 5 to 10 kg. Sharing of the duiker lasted for 3.5 h and accounted for the longest food-sharing episode observed during this study. The remains consisted of a large piece of skin and bone fragments from the limbs and cranium. During the major part of the episode owner and recipients alternately took blood, meat, and bone from the partly opened carcass. Eighty seven minutes after onset of observation, the prey was partly dissected, the recipients had received larger pieces of meat, and sharing continued. Opening of the cranium and consumption of the brain took place approximately 180 minutes

Figure 5.1: Type of Food and Duration of Food Sharing Among Bonobos at Lomako

Food	**Duration (min)**	**First Owner**	**Recipient**	**Second Owner**	**Recipient**
meat	>29	F	2F (1)	–	–
meat	218	F	1M/2F (3)	F	(3)
Anonidium	>15	F	1M/1F (2)	–	–
Anonidium	90	F	(1)	–	–
Treculia	75	1M	–	1F	1M/2F (3)
"	65	1F	2F	–	–
"	82	1F	(3)	1F	–
"	81	1F	2F	1F	2F (2)
"	>92	1M	1F (1)	1F	(1)
"	>80	1F	2F (2)	–	–
"	>10	1F	1F	–	–
"	43	1F	3F (3)	–	–
"	6	1F	(1)	–	–
"	>20	1F	1F	–	–
"	90	1M	2F (3)	1F	1M/2F (3)
"	127	1F	1M/1F (2)	–	–
"	>57	1F	2F	–	–
"	61	1F	1F (2)	–	–
"	46	1M	1F	1F	–
"	53	1F	1F (1)	1F	(1)
"	>25	1F	1M/1F	–	–

F=female, M=male, figures in brackets refer to the number of immatures

after onset of observation, following transfer of the prey to another adult female. During the entire episode, all three infants present had free access to the prey and removed small pieces from the mouth or hand of adults or directly from the prey.

Time for sharing plant food varied from 6 to 130 minutes (x=62.4, SD=35.9, n=20). The episodes reported on here involved two tree species, *Treculia africana* and *Anonidium mannii,* producing fruits of extraordinary large size and weight. From *Treculia* the bonobos preferably ate the seeds, but occasionally the fibers embedding the seeds were consumed as well. Fresh *Treculia* fruits had an average weight of 7.6 kg (range: 5-30 kg, SD=6.6, n=25) and a mean diameter of 24.3 cm (range: 19-45, SD=5.7, n=25). In one fresh fruit, seeds accounted for 10.9 percent of the total weight (7 kg). Except for one episode, bonobos did not choose *Treculia* fruits still hanging on the tree but consumed fruits lying on the ground. In case of *Anonidium,* only the juicy pericarp was eaten, and bonobos were seen to eat fruits still hanging on the tree as well as fruits lying on the ground. Comparative data on size and weight for *Anonidium* are not available from Lomako, but according to the studies by Hladik and Hladik (1990) fruits may weigh up to 10 kg.

Within and between episodes variation of the mode of food sharing was high. Looking for typical features, three modes of sharing were distinguished: (1) Removing pieces of food directly from the owner's fruit, (2) taking food from the hand of the owner, (3) taking chewed food from the owner's mouth (Figure 5.2). Only in one case of food sharing (not included in the data presented here) did we observe a juvenile female passing the fruit of *Irvingia gabonensis* to an immature male.

Figure 5.2: An adult female (right) carrying a *Treculia* fruit. Another female (left) is begging for food by extending her hand toward the owner's mouth.

Sexual behavior occurred during eight episodes, and the total number of sexual interactions was twenty-one. The majority (fifteen cases) accounted for genito-genital rubbing among female owners and recipients. Heterosexual copulations occurred five times, three times between a male owner and a female participant and twice vice versa. Following copulation, food was transferred from males to females three times. However, in another case a male owner copulated seven times in close succession with a female vigorously begging for *Treculia* but did not share the fruit.

When sharing meat or plant foods adult recipients frequently made begging gestures, facial expressions, and related vocalizations. Begging by adults clearly resembled the behavior of infants directed to their mothers. The data currently available did not permit a quantitative analysis of the amount and intensity of begging behavior.

However, there seemed to be a correlation between intensity of begging and party size, with members of larger parties begging less often, less intensely, and for shorter periods of time compared to members of small parties.

During meat sharing, agonistic interactions were entirely absent (first episode) or mild (second episode) and restricted to displacements of potential participants by the owner (n=4) or other recipients (n=6). During sharing of plant foods agonistic interactions were also rare (n=19). However, in one episode two adult females repeatedly made joint attacks on adult males approaching a group of three females with infants and one male who were involved in food division.

Figure 5.3 includes data on party size and adult sex ratio. Mean size of food sharing parties (including owner, recipients and all individuals present but not participating) was slightly higher but still within the range of average party size (8.1 vs. 6.9).

Figure 5.3. Party Size and Sex Ratio

	Average party at day time	**Food sharing party**	**Number of FS-individ.**
n	100	10	21
party size	6.93	8.1	3.1
	(3.29)	(2.38)	(1.36)
sex ratio	0.68	0.70	0.90
	(0.23)	(0.15)	(0.15)

Mean values and standard deviation (in brackets) for party size and sex ratio. Left= day parties; middle= food-sharing parties, including owner, participants, and bystanders. The third figure (right) refers to the group consisting of owner and recipients only.

The corresponding figure in the third column shows, however, that only a small faction of a food-sharing party was actively involved in food sharing (8.1 vs. 3.1). The adult sex ratio within food sharing parties was very similar to parties not engaged in food sharing, and in both cases there was a pronounced bias in favor of females. This bias was most prominent in the factions of parties actually involved in food sharing where the number of females was more than five times higher than the number of males.

Figure 5.1 shows that in most cases (seventeen) the food that was divided was in possession of adult females, and in the four cases involving male owners food was later transferred to females. Figure 5.3 shows that on average five members of food-sharing parties were not involved in food sharing, and that the proportion of males present but not participating in food division was higher compared to females.

In order to assess both frequency and direction of food exchange within food-sharing parties, the twenty-one episodes of food-sharing were split into dyads (Figure 5.4).

Figure 5.4. Frequency and Type of Involvement in Food Sharing by Mature Males, Mature Females and Immatures of Both Sexes

<table>
<tr><th></th><th colspan="4">Recipient</th></tr>
<tr><th>Owner</th><th></th><th></th><th colspan="2">Immatures</th></tr>
<tr><th></th><th>Male</th><th>Female</th><th>Other</th><th>Own</th></tr>
<tr><td>Female</td><td>7</td><td>31</td><td>20</td><td>13</td></tr>
<tr><td>Male</td><td>0</td><td>4</td><td colspan="2">4</td></tr>
<tr><td>Immatures</td><td>0</td><td>0</td><td colspan="2">1</td></tr>
</table>

The results pictured in Figure 5.4 show that female owners (n=71) shared most often with other females, frequently with immatures (own and offspring of other females), and least frequently with males. For a realistic calculation of the frequency with which males and females are involved in food sharing, it is necessary to consider the adult sex ratio within parties shown in Figure 5.3. Relating this figure to the total of forty-two dyads involving mature individuals, expected frequency of ownership would be fourteen for males and twenty-eight for females. Due to the low frequency of male participation, the observed frequencies differ significantly ($Chi^2 = 10.7$, $p < 0.001$) from the expected values.

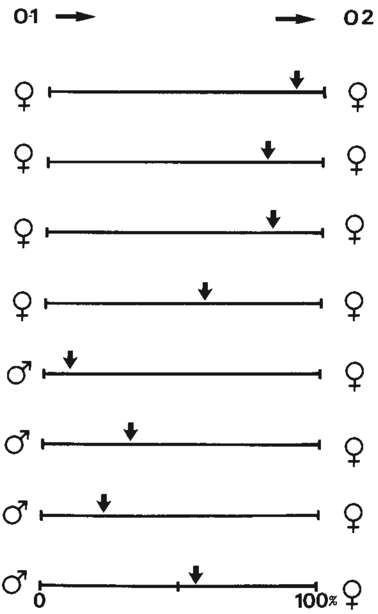


Figure 5.5: Timing of transfer of food from owner 1 (01) to owner 2 (02). The vertical arrows indicate the relative time of transfer in relation to the total duration of the food sharing episode (100 percent).

Changes in ownership of dividable food occurred eight times. Only in one case was the transfer of food accompanied by aggressive interactions between the original and second owner. In three cases the transfer (from males to females) coincided with mating between the first (male) and second (female) owner. Figure 5.5 shows the relative time of transfer of food from one to another individual. All transfers between females occurred during the second half of the episode, suggesting that females tended to make small sacrifices when transferring food. Transfers from males to females occurred at earlier times. However, these differences are not significant (Mann-Whitney-U-test, U=2, n.s.).

Figure 5.6. Feeding on *Treculia Africana* Without Food Sharing

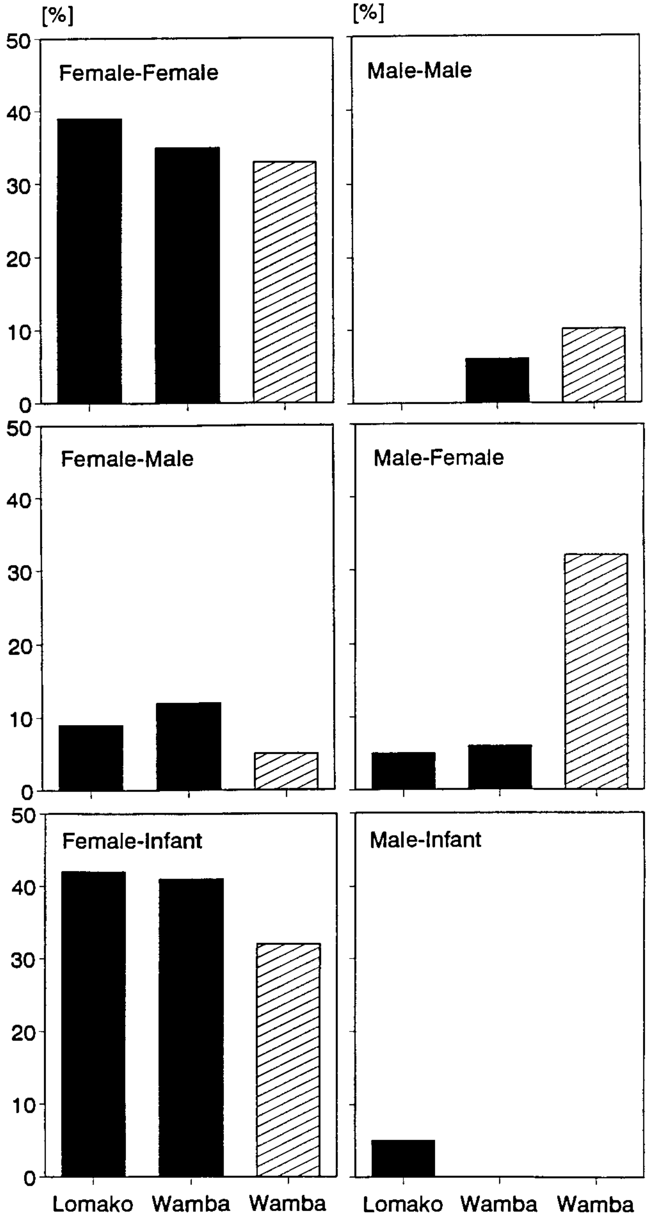
Sex of Owner	**Duration (min)**	**Sharing (yes/no)**	**Begging (yes/no)**
M	>60	+	–
M	>69	+	+
M	>30	+	–
M	>51	+	–
M	>58	+	–
M	>17	–	+
M	>9	–	–
M	?	+	–
M	>5	+	–
F	>10	+	–
F	>10	+	–
F	>30	+	–
F	?	–	–
F	>65	+	–
F	>43	+	–

Fifteen cases recorded for males (M) and females (F) feeding on *Treculia africana* without food sharing. In twelve cases, other individuals simultaneously share food at the same site. In two cases other individuals begged the owner for food but did not succeed in receiving it.

Figure 5.6 shows the number of single individuals feeding separately but parallel to episodes of *Treculia* sharing by other party members. The results show that males fed solitarily more often and for slightly longer times (x=37.4 min, n=9) than females (x=31.6 min, n=6).

Figure 5.7 shows the respective rates of plant food sharing between members of different age/sex classes collected at Lomako (this study) and at Wamba (Kuroda 1984). To make the data from both studies compatible, the relative frequencies of dyadic food exchanges were compared, using the figures from successful food interaction units (FIU+) presented in Table II of the paper by Kuroda (1984), and the data shown in Figure 5.4 of this chapter. Considering only natural food, the results of both study sites are similar. However, the figures for the division of artificial food collected at Wamba (Kuroda 1984; Table V) differ markedly from those for natural food. In this case, male owners share more often with both male and female recipients.

Figure 5.7: Frequencies of division of food sharing between individuals of different ages and sexes. The first two bars (black) refer to the sharing of natural plant foods observed in Lomako (this study) and Wamba (Kuroda 1984), respectively. The third bar (hatched) refers to Kuroda's data (1984) on the sharing of provisioned food among bonobos at Wamba.



Discussion

The observations on food sharing among bonobos at Lomako described above can be summarized as follows: (1) bonobos shared both plant foods and meat, (2) with one exception (the first case of meat sharing), the food items divided were large and heavy, (3) food sharing generally involved individuals of different ages and sexes, but females were more often in possession of food and shared food more often than males, (4) female possessors most frequently shared with infants, often with mature females, and least frequently with mature males, (5) infants received/took food more often from females other than their mothers, (6) food was transferred from males to females and among females with equivalent rates, but never from females to males or among males.

Provided these results are representative features of food sharing among bonobos, the following questions arise: (1) why do females share food more frequently than males? (2) why do they share so often with infants of other females ? (3) what are the possible reasons for the observed asymmetries in direction and timing of food transfer?

Possible answers to the first question could be that males and females have different food preferences or males travel more often alone (or in male bands) than together with females, and therefore have a lower chance of participating in sharing of food obtained and divided among females. Comparison of the data on food sharing with those collected for solo feeding on *Treculia* (Figure 5.1 and 5.6) demonstrate that both sexes fed on it at rather equal rates. Moreover, the figures of Figure 5.6 indicate that, except for two cases, males fed solitarily when other individuals shared food simultaneously at the same site, and other individuals rarely begged for food from males feeding solitarily. A possible explanation of the low rate of begging for food from males could be that females possessed the better (larger/heavier) food items. The data available are not sufficient to analyze this aspect. Comparing the time of food consumption between individuals who fed solitarily and those who shared with others, the former fed significantly longer than the latter (x=51 vs. 35 min.). However, instead of being related to the size/weight of the food consumed, distinct feeding strategies seem to cause the difference in feeding time. The longer duration of consumption during sharing may be related to the reluctance of the owner to share with recipients and the modes of food distribution. Hence, there is no evidence supporting the assumption that the observed differences in food sharing express sex-related food preferences.

Did males travel more often alone (or in all-male parties) than with females? Counts of party size obtained during this study ranged between one and sixteen animals (x=5.2, SD=3.33, n=247) and the average adult sex ratio of parties was 0.51. Considering sex and total number of the individuals (except dependent infants) identified during this study, the adult sex ratio within the Eyengo community was 0.5 (eight males, fourteen females). Hence, male presence in parties corresponds well with the number of males within the community. Accordingly, males and females had equal chance to participate in food sharing.

Another possible explanation for the comparatively low rate of food sharing among males would be that the benefits gained by females exceed that of males. Division of food entails costs to the owner. According to the paradigm of sociobiology, sharing should be restricted to close kin, or else costs should be balanced by one or the other form of reciprocity (Trivers 1971). Reports from the long-term study at Wamba provide the best source of information on migration patterns available. Here, female bonobos are exogamous and males philopatric (Kano 1982). Provided the bonobos at Lomako follow the same migration patterns, kin selection does not offer a satisfying explanation, because sharing among non-kin (females) by far exceeds sharing among close kin (males). What remains is the question whether or not female community members reciprocate in food division. Unfortunately, the data necessary to analyze this aspect are not yet available. However, even in the case of a positive answer, this would not explain why males (close kin) behave so differently.

Previous studies established that in spite of the flexibility of parties, comparatively stable relationships exist among adult females, but not among males (White 1989). Although similar social ties may also be found among particular males (our observations) as well as among males and females (Kano 1982; Furuichi 1989; Kuroda 1989), data from our study are in general agreement with White's (1989) observation. It has been hypothesized that the cohesion among female bonobos may be related to defense of food resources (White 1989; Parish 1993). Observations of females collectively charging a male who owned dividable food or attempting to join a food-sharing party (see above) clearly demonstrate the ability of females to defend food resources. Parish proposed that the formation of affiliative bonds among females raises their status above those of group males (1993). Results of our study at Lomako suggest a similar tendency. However, within the group of adult females, the data collected in this study did not indicate a consistent correlation between social status and ownership of food. A group of five females who was thought to have a high social status within the community were perhaps more often in possession of food than other individuals, but within this group the role of ownership occurred with rather equal rates. It is therefore suggested that social bonding among female bonobos facilitates monopolization of food resources. Within this system, the relative status of individual females may be less important than the stability of temporary female alliances. Females who share more often with other females may reinforce existing bonds and recruit new allies. By contrast even in the few cases where parties had more than one male, males did not cooperate or share food with others.

Considering the comparatively low cost for acquisition of a *Treculia* or *Anonidium* fruit, its very large size, and the small amount of food removed by an infant, costs for an individual (Ego) sharing with an infant of another female may be almost negligible. The mother of the infant participating in eating food owned by Ego also benefits (via inclusive fitness), even if she does not receive any food. If monopolization of a food patch depends on the number of females present (White and Wrangham 1988; Wrangham 1980), Egos' ability to keep other individuals at bay may be crucial. The act of sharing with the infant of other females may be a compromise between costs (food consumed by the infant) and benefits (the presence of another female). However, the infant's mother remaining at the feeding site does not only enable her infant to consume food owned by others, but may also increase her chance to take over part of the food from the original owner. At least five cases observed during this study support this assumption. In another three cases, females attending a food-sharing party without direct participation eventually acquired small morsels by snatching it from their own infants.

Attempts to explain the few food transfers from males to females are difficult for the following reasons. First, the number of cases observed was very low (n=4), and each case involved different individuals. Second, variability in the duration of food division, the time of transfer, and the related interactions was high. In one case change of ownership occurred when two adult females charged the male owner, while in the other three cases the fruit was transferred immediately after copulation between the original (male) and second (female) owner. Considering the time spent feeding after food transfer, females acquired a large share of the food item initially owned by the male. It should be noted that in three cases, males did not participate in feeding on that food after transfer and the female owner fed solitarily (n=1) or shared with another female (n=2).

Males accepted the loss of a significant amount of food without any intervention, and this requires some explanation. The first case seems to be simple: the two females charged the male who abandoned the fruit. The two other males present did not render any support. One of them participated later in food division with the females, and the other remained close to the food-sharing party but did not receive any food. Hence, this transfer was obviously the result of cooperation among females and the lack of male alliances. In the other three cases, transfer of food was preceded by mating. Since mating increases the chance of pregnancy and paternity, males who have just copulated with a female may not compete with her over food because if copulations are a common strategy to receive food from males, the female may immediately switch to a second male and offer another copulation if the first male does not share. In this case, males who copulate but do not share may diminish an immediate chance for increasing their reproductive success. Also, a male who does not share food with a female shortly after copulation may continue to deprive the female of food later during pregnancy, when optimal nutrition will be crucial for the fetus. Consequently, the female may avoid mating with such a male in the future. Hence, the transfer of food from males to females shortly after copulation may directly and indirectly increase the reproductive success of males.

Data on food sharing among bonobos from another study site (Wamba) have been published by Kano (1980) and Kuroda (1984). Obvious differences exist with respect to meat consumption. At Wamba bonobos hunt less frequently than they do at Lomako and capture only small prey like flying squirrels (*Uromastyx sp*). Moreover, although begging for meat has been seen, bonobos at Wamba have not yet been observed to share meat (Ihobe 1992). As shown in Figure 5.7, the patterns of sharing natural plant foods are very similar at both sites. Striking differences become apparent, however, when comparing the results of the sharing of natural foods from both places with the data collected at the artificial feeding site at Wamba (Kuroda 1984). Figure 5.7 shows that when feeding on sugar cane, males at Wamba shared more often with both males and females than they did in the case of natural food. The large amount of food, its high predictability, the low costs of acquisition, and the setting of the artificial feeding site may have had severe affects on the size and composition of visiting parties. Differences in size and composition of these parties may in turn explain the observed differences in behavioral interactions, including the frequency of food sharing (White 1989).

Considering the information available from the different studies of the two *Pan* species, the sharing of food among bonobos on one hand and among chimpanzees on the other have many features in common (for bonobos see Badrian and Malenky 1984; and Kano 1992; for chimpanzees see Feistner and McGrew 1989; McGrew

1992). Striking differences seem to exist concerning the general type of food divided: while most cases of food sharing among bonobos involved plant food, it is thought that chimpanzees share predominantly meat. Asymmetries between the two species can also be found in the (1) overall frequency of food sharing, (2) participation of males and females in food sharing episodes, and (3) distribution of roles (owner, participant) among males and females.

There are different opinions about the frequencies of meat sharing and division of plant foods among chimpanzees but no supporting data. While McGrew (1975, 1992), Nishida (1970) and Silk (1978) have argued that division of plant foods is more common, Teleki (1973) and others propose that meat sharing is more prominent. Whatever the case may be, most authors agree that among chimpanzees division of plant food occurs most frequently between mother and infant and involves food items difficult to procure and/or manipulate by the infant (McGrew 1975; Silk 1978, 1979; Boesch and Boesch 1989). Hence, the patterns of food sharing among chimpanzees on one hand and bonobos on the other differ most prominently concerning the division of plant foods. The two fruits, *Treculia* and *Anonidium*, frequently shared among bonobos at Lomako are also available at the Tai National Park, and chimpanzees are known to eat and share *Treculia* (Boesch and Boesch 1984). When more data on the mode and frequency of *Treculia* sharing among Tai chimpanzees is available, the patterns of food sharing in the two *Pan* species may become even more similar. Considering the high degree of variability of food preferences, hunting activities, and modes of food acquisition reported for different communities of chimpanzees (e.g. Kawanaka 1982; Wrangham and Riss 1990), the real distinction of food-sharing between chimpanzees on one hand and bonobos on the other may be found in the composition of food sharing parties and the direction of food division rather than in the relative amount of meat or plant foods shared. Using data on meat sharing among chimpanzees, McGrew (this volume) shows the relationship between status, fertility, and health on one hand, and nutrition, diet, and status on the other. In chimpanzees, females get food mainly from adult males, and the amount of food received is correlated with higher reproductive success in females. In bonobos, it is the females who regulate the flow of food to other individuals. Considering the possible impact of the amount of food on the birthrate, food sharing could be a major device for competition among female bonobos.

The data on food sharing among bonobos presented here are based on a small sample size. More comprehensive studies are required to understand the social factors regulating food exchange and the benefits promoting this behavior. Future analyses of the nutritional value of the fruits as well as competition between bonobos and other large mammals for these particular food items may shed further light on these issues. However, even in this preliminary stage the data presented have some interesting implications. It has been proposed that food sharing among higher primates is essentially associated with hunting behavior (e.g. Etkin 1954; Tooby and DeVore 1987). However, consistent with conclusions from previous studies (Kavanagh 1972; McGrew 1975), the observations on bonobos presented above indicate that neither hunting nor meat consumption is a necessary precondition for food sharing. Moreover, contrary to previous reports from chimpanzees (e.g. McGrew 1975), division of plant food is not restricted to mother-infant dyads nor to close kin. Instead, it occurs most frequently among adult females, the faction within the community with the weakest kinship bonds.

Notes

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