

Food sharing in wild pygmy chimpanzees, *Pan paniscus*

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Food sharing is especially well-developed in the genus *Pan* and has been observed in both field and captive studies in chimpanzees, *Pan troglodytes* (Goodall, 1968; 1986; McGrew, 1975; Nishida, 1970; de Waal, 1989) and bonobos or pygmy chimpanzees, *Pan paniscus* (Kano, 1980; Kuroda, 1984). Three hypotheses have been advanced to explain the evolution of food sharing among non-relatives. The sharing under pressure hypothesis was developed from observations that attacks and displays at an individual with meat, although rarely successful, greatly reduced the ability of the possessor to feed (Wrangham, 1975). By sharing with others, the possessor would be able to forestall this disturbance and be able to feed on at least part of the kill.

Food sharing to enhance status hypothesis (Moore, 1984) proposes that individuals share food with those of higher rank in order to gain status.

The reciprocity hypothesis (Trivers, 1971; de Waal, 1989) argues that individuals share food in return for reciprocal food sharing or some other return currency such as mating opportunities in the future. Observations of wild and captive bonobos support reciprocity in the sharing of food in return for sexual favors (Kuroda, 1984; de Waal, 1989). In a captive study, de Waal found support for the reciprocity hypothesis in chimpanzees in their patterns of sharing of bundles of edible branches.

Plant foods, both natural and provisioned, are rarely shared by adult chimpanzees in the wild but are shared by mothers with their dependent offspring, and are generally difficult food items to open or process (Nishida, 1970; McGrew, 1975; Silk, 1978; Goodall, 1986; Hiraiwa-Hasegawa, 1990). Provisioned bananas are also shared by mothers with their offspring and by males with females (McGrew, 1975). Among chimpanzees, meat is almost always shared, mostly among males and between males and females (Teleki, 1973; Wrangham, 1975; Goodall, 1986; Boesch & Boesch, 1989). Many individuals receive meat from a carcass, even if it is not a large food item (mean: 8 individuals, range 4 to 15, Teleki, 1973).

In contrast to chimpanzees, bonobos share plant food among adult females (Kano, 1980; Kuroda, 1984). Large, naturally occurring fruits are shared mostly among females (n=52) and rarely by adult females with males (n=30) or among males (n=7, total 90 observations). Readily accessible small plant food items are shared predominantly by mothers with infants and juveniles (84 out of 85 observations). Provisioned sugar cane is mostly shared by adult females with adolescents, juveniles, and infants (60 out of 85 observations). No meat sharing has been reported from Wamba (Kano, 1980).

In his captive study, de Waal (1989) reports that high-energy food items, such as bananas, provoked physical violence among chimpanzees. This suggests that the three different food sharing hypotheses are not mutually exclusive for chimpanzees but may reflect different types of sharing that occur for foods of different quality. The sharing under pressure hypotheses may be most appropriate to high quality or highly prized food items such as meat (Wrangham, 1975). Sharing to enhance status may presumably be most applicable under special circumstances, for example during status changes where an individual has access to some restricted resource (de Waal, 1982). This interpretation is supported by observations that high-ranking males were more able to obtain meat from possessors than were low-ranking males (Wrangham, 1975), although this does not preclude reciprocal sharing, especially for some other currency such as support, or sharing under pressure. Sharing by dominants with subordinates is best explained by reciprocal sharing (de Waal, 1989).

This paper reports preliminary accounts of fruit and meat sharing among the non-provisioned pygmy chimpanzees of the Lomako Forest of central Zaïre, and examines the difference in sharing and begging behaviors associated with a highly prized food item (duiker meat) with observations of fruit sharing. Comparisons are made with chimpanzee food sharing and the implications for the three food sharing hypotheses are examined.

Methods

The data presented come from studies of *Pan paniscus* in the Lomako Forest of central Zaïre from 1983 to 1985 and 1991. The study site is principally composed of undisturbed, polyspecific, climax evergreen forest intermixed with smaller amounts of secondary growth, slope forest, and swamp forest (White, 1992b). Descriptions of the study site and population are given elsewhere (Badrian & Badrian, 1984; Badrian & Malenky, 1984; Thompson-Handler et al., 1984; White, 1988, 1992a, 1992b).

Food sharing was defined as two or more individuals obtaining food from the same single food item. It does not include infants taking chewed foods from the mouth of their mothers. Sharing was sometimes preceded by begging. The following soliciting begging behaviors were observed: a) Approach to sit usually in contact with the possessor, an approach was usually followed by other soliciting behaviors; b) Direct stare at the possessor by the soliciting individual, often from close range (10 cm between faces); c) Slow reach by the soliciting individual toward the food item without touching either the food or the possessor, usually with palm down (all age classes), but occasionally with palm up (infants only); d) Touching the food item, often with a direct stare at the possessor; e) Grabbing at the food item, this was a rapid movement, unlike reaching, and the solicitor would attempt to pull part or all of the food item away from the possessor; f) Penis presentation, males would approach and sit close by with arched back, legs spread and present an erect penis to the possessor.

The size and composition of the party at the time of the sharing, duration of sharing and feeding bout, and the height of the sharers were recorded. Age and sex classes were as defined by White (1988). Fresh samples of both shared and non-shared fruits were collected and weighed the same day. Where possible, five fruits were weighed and the mean weight used. It was not possible to obtain five sample fruits for the largest three fruit species as these were rarely found ripe and intact on the ground.

Frequencies were compared with G-tests of independence and goodness of fit G-tests with Williams correction. Correlations were non-parametric Kendall coefficients of rank correlation corrected for ties (Sokal & Rohlf, 1981).

Results

Food sharing was observed at total of 32 times in 363 h of observation. Observations of sharing were not evenly distributed among field seasons: 24 sharings were observed during the 43 h and 25 min of observation time of the 1991 field season. Fruit was shared 24 times and meat from a young *Cephalophus nigrifrons* duiker was shared 8 times. The meat sharing events are all from a single kill observed in 1991.

Two species of fruit were observed being shared: *Treculia africana*, (mean weight 8.9 kg, n=2) was shared 21 times, and *Carpodinus gentilii* (weight 0.9 kg, n=1) was shared 3 times. *Anonidium mannii* (weight 2.9 kg, n=1) is known to be shared at Wamba and feeding remains at Lomako suggest sharing although no direct observations of sharing were made (several sitting depressions with fragmented, chewed parts of fruit surrounding each sitting site). The mean size of fruit eaten by focal animals during these study was 452 g (range 0.34-8875 g, n=23)(Fig. 1). Only the three large fruits are known to be shared. *Treculia* and *Anonidium* require no special preparation as they have only a very thin, soft skin (less than 1 mm). *Carpodinus*, in contrast, has

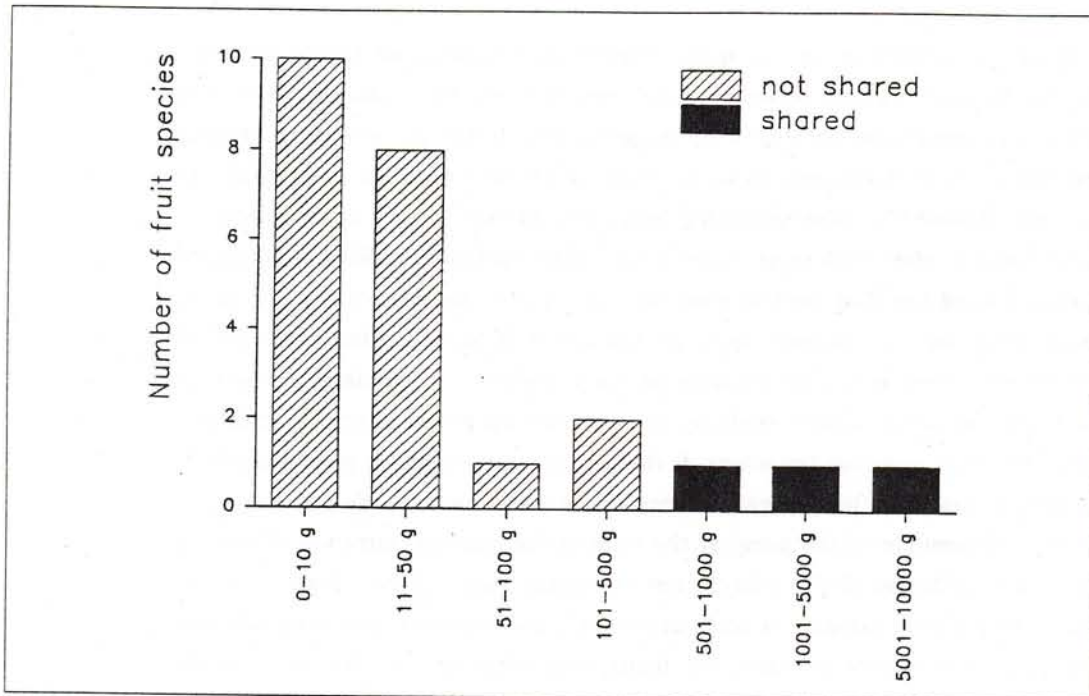


Fig. 1. Distribution of size of fruits eaten by focal animals. *Anonidium mannii* (2.9 kg), which was not eaten during focal sampling, has been added (see text).

a thick, hard skin (24 mm thick) and the fruit was prepared by adults by biting off a segment of the exocarp and scooping out the soft contents with the fingers.

Four instances of fruit sharing were observed on the ground. All other observations of sharing took place in the trees above a height of 11 m. The modal height class was 11 to 15 m for sharing fruit and 20 to 25 m for sharing meat. There was no correlation between party size and the frequency of either begging ($t=.47$, n.s., $n=7$) or sharing ($t=.42$, n.s., $n=7$).

The ratio of begging to sharing was not significantly dependent on the species of fruit ($G=1.06$, n.s.) but was significantly dependent on whether the feeding was on fruit or meat ($G=22.51$, $p<.001$). When compared to an expected distribution of begging frequency based on the duration of sightings in which begging or sharing occurred, both begging behaviors and sharing occurred significantly differently from expected frequencies (begging, $G=50.55$, $p<.001$; sharing, $G=14.13$, $p<.001$). The rates of soliciting behaviors were higher for meat than for the two fruit species, but the rates of sharing were highest for one fruit species and lowest for the other fruit species (begging rates: meat, 43.63 per hour; *Treculia*, 11.57; *Carpodinus*, 4.07; sharing rates: meat, 5.45 per hour; *Treculia*, 15.18; *Carpodinus*, 2.03).

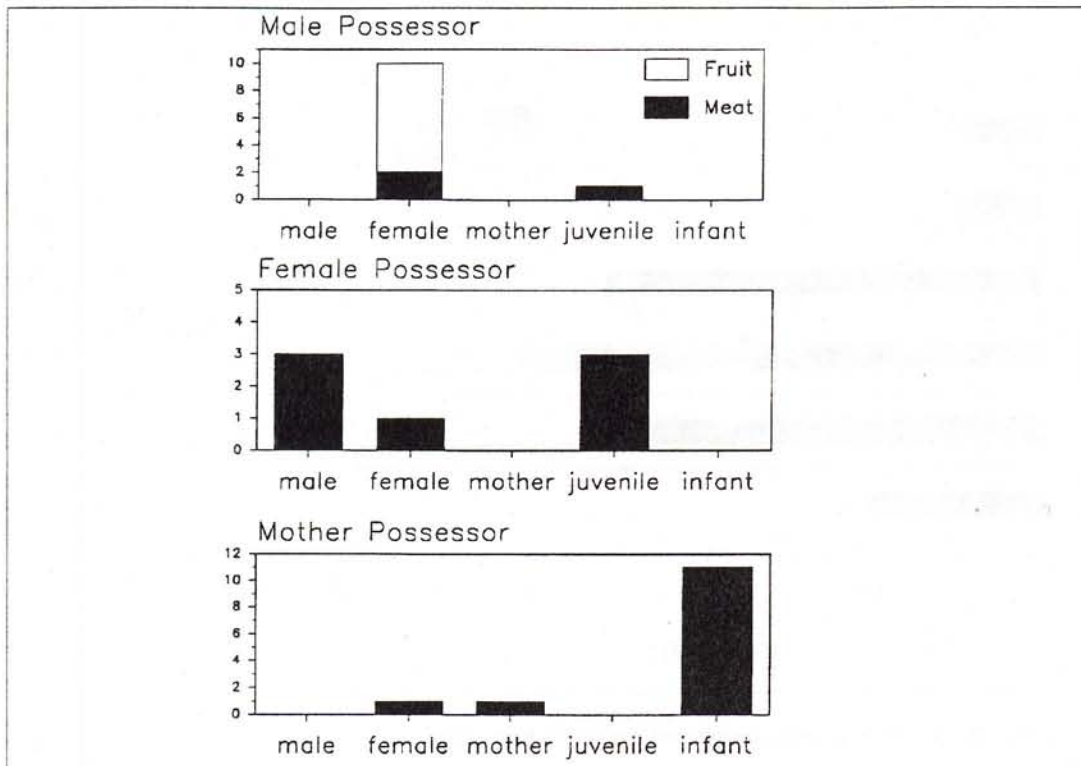


Fig. 2. Frequency distributions of sharing dyads among age and sex classes.

The mean number of individuals that shared the same food item at the same time was 2.03 ($n=30$, range 2-3), but a single *Treculia* fruit was fed from by a sequence of 7 individuals (2 adult females, 3 adult males, 1 subadult male, 1 juvenile female) before being totally fragmented or consumed. The mean duration of a food sharing event, excluding giving pieces of a food item, was 10.33 min for fruit ($n=3$) and 1.25 min for meat ($n=4$).

During meat sharing, the party size was 7 independent individuals (4 adult males, 2 adult females, 1 juvenile female). The meat was eaten by a single adult male who shared mostly with one of the females (7 of 8 shares)(Fig. 2). The adult female obtained possession of the carcass after 47 min when the male had consumed the brain, some internal organs, and most of one hind limb. After 32 min, when the female had consumed most of the remaining meat, the party descended into a thick vine tangle where observation conditions were poor and it was not possible to determine definitively who was feeding. While on the ground the remainder of the carcass was consumed, leaving only the lower jaws, a piece of brain case, one knee joint and the lower intestine.

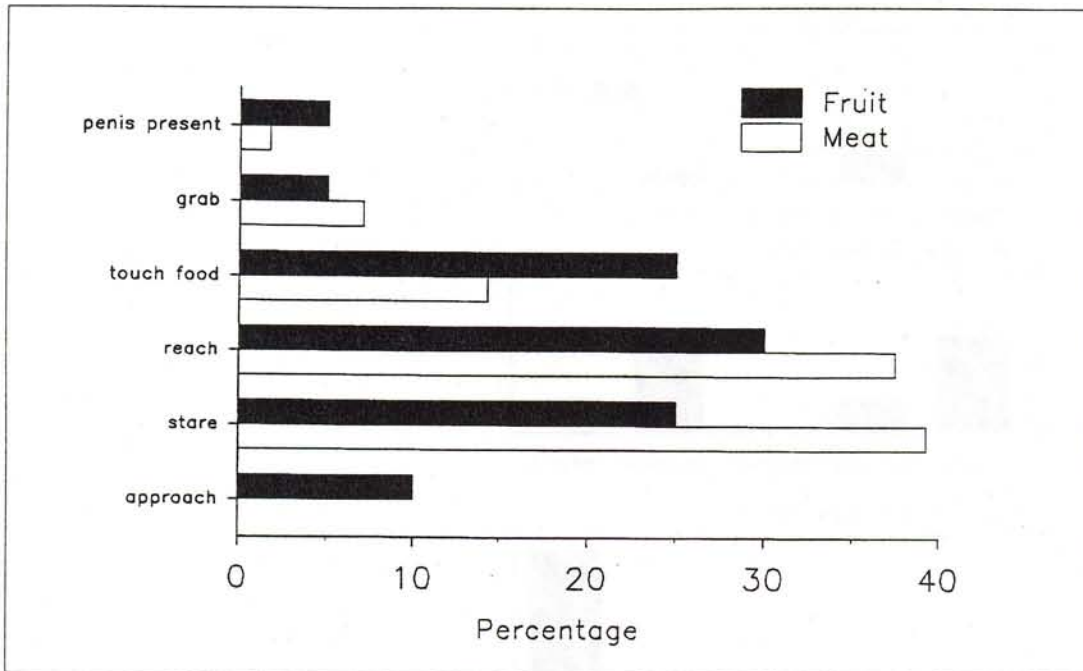


Fig. 3. Types of begging behaviors for meat and fruit.

Males shared fruit with females and a juvenile, but not with other males. Females without infants shared fruit with males, with juveniles, and with a female with an infant. Females with infants shared mostly with their infants, but also with other females. The frequencies of types of soliciting behaviors were similar for fruit and meat eating was not significantly different (pooling 'approach' and 'stare' to remove zeros: $G=1.61$, n.s.)(Fig. 3). The most frequent begging behaviors were reaching and staring. Two penis presentations were performed to females. Most begging was performed by adult females without infants for meat (47 of 50 solicitations, total number of begs: 76). Adult males were observed to beg 7 times, mostly for fruit ($n=6$).

Food sharing without begging was common between mothers and infants (8 of 11 shares) but rare between adults (2 adult female to male, 2 adult male to adult female, 1 adult male to juvenile, 1 adult female to juvenile).

Begging was ignored or refused (by turning away) on 59 occasions. Most of these were during the meat feeding when the possessing male refused the solicitations of an adult female ($n=41$). During this bout, the male also refused two solicitations from an adult male and six from a juvenile female. When in possession of the carcass, the adult female refused solicitations from an adult

male (n=2), an adult female (n=1), a subadult male (n=2), and a juvenile female (n=2).

Only one aggressive interaction over a single food item was observed, when two males fought for the possession of a single *Treculia* fruit as females were approaching. Only one GG rubbing was observed associated with sharing, by two females who did not share at that time although one of them did share with the possessing female later in the observation.

Discussion

The relative infrequency of food sharing among Lomako bonobos is interesting especially compared with the markedly uneven distribution among field seasons. It is possible that this difference is a reflection of increased habituation, especially if most sharing occurred on the ground where observation conditions are difficult, and especially if the individuals are less habituated. Most sharing, however, occurred in the trees. An alternative explanation for the uneven distribution is the availability of food suitable for sharing. *Treculia* does not appear to fruit annually, and each tree produces only a few fruits, so that these fruits are only occasionally available. Both *Treculia* and *Carpodinus* were in fruit during the 1991 field season. Previous field seasons included one *Treculia* fruiting (in 1985), and sharing of fruit was also observed at this time. *Carpodinus* fruiting seasons were, however, observed in previous fruiting seasons, but less sharing was observed. All but one observation of *Carpodinus* sharing was between mothers and infants and, in previous seasons, observations of *Carpodinus* feeding was of parties with no infants. Feeding on duikers is clearly an uncommon event and has only been observed a total of 4 times in the 11 years of the Lomako Forest Pygmy Chimpanzee Project (Thompson-Handler & Malenky, pers. comm.).

Only the three largest of the fruits are known to be shared at Lomako. Of these three fruits, only the smallest, *Carpodinus*, required special preparation and was mostly opened by mothers who then shared the contents with their offspring. These fruits may contain too little food to warrant sharing among adults. The single observation of adult sharing of *Carpodinus* was between an immigrating female and an adult male with whom she had recently begun a close association. As has been observed for the chimpanzees at Mahale, bonobo mothers also share easy to process foods such as *Treculia* with their infants (Hiraiwa-Hasegawa, 1990).

Based on the high rates of begging and lower rates of sharing, meat does appear to be a highly prized food item. This preference is not reflected,

however, in more intense types of begging behaviors, more sharing, or escalation of aggression.

Food sharing among bonobos at Wamba appears to be more frequent than at Lomako. Kano (1980) observed 261 sharing events of 11 food species, 10 of which were naturally occurring foods. 86 sharing events were of provisioned sugar cane. Kuroda (1984) reports 60 sharing events of natural food and 509 sharings of artificially provided foods in 427 hours of observation away from and 165 hours at the artificial feeding site. Both authors, however, include observations of an infant taking processed food from its mother's mouth and feeding on the same food branch in their analyses. These types of sharing were not included in this analysis. Of the 17 naturally occurring plant foods that have been observed being shared at Wamba (Kano, 1980; Kuroda, 1984), 9 species are also eaten at Lomako but have not been seen to be shared.

As in this study, Kano (1980) and Kuroda (1984) observed frequent sharing between males and females and among females. They also observed some sharing among males, which was not observed at Lomako. Differences in food sharing between Lomako and Wamba may reflect the impact of provisioning or differences in party sizes and compositions. Parties are large at Wamba, but the lack of a relationship between begging or sharing and party size at Lomako suggests that this may not explain any differences.

Unlike chimpanzees, bonobos at both Wamba and Lomako frequently share plant food among adults. This may be related to the presence of large fruits in central Zaïre that are not available in chimpanzee habitat as well as the major differences in social organization between the male-bonded chimpanzee (Nishida, 1970; Wrangham, 1975; Goodall, 1986) and the more female-based bonobo social system with stronger ties between males and females (Kano, 1980, 1982; Kuroda, 1979, 1980, 1984; Kitamura, 1983; White, 1988, 1989, 1992a).

Unlike in chimpanzees, there was no male-male sharing in the one sighting of meat eating by bonobos as well as no male-male aggression, even though there were several males present that were clearly interested in the carcass. Male bonobos at Lomako also did not share fruit. In contrast to meat-sharing chimpanzees, this suggests that the sharing under pressure interpretation of male-male meat sharing is not applicable to bonobos. This difference may be related to the relatively weak affiliation and lack of strong alliance formation among male bonobos. A single male is, therefore, not threatened by male-male alliances and does not need to reinforce male-male bonding and cooperation through sharing.

The frequent sharing by males with females may reflect a form of reciprocal sharing where the return currency may be return sharing or future sexual access. Although mating was not observed during sharing, males did share with females without infants and not with females with infants. These females were the most likely to reciprocate, as mothers shared mostly with their offspring, and the most likely to be reproductive. Females may share with males to gain status with a dominant individual or for reciprocity, but it is interesting that the female refused to share the meat with the adult males in the party despite their solicitations. This implies that females are also not subject to sharing under pressure.

These interpretations are, however, based on only few observations of fruit sharing, and only one observation of meat eating. Any conclusions and interpretations must, therefore, be tentative until more data become available.

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References

- Badrian, A.J. & Badrian, N.L. (1984). Group composition and social structure of *Pan paniscus* in the Lomako Forest. In Susman, R.L. (ed.), *The pygmy chimpanzee: Evolutionary biology and behavior*, Plenum Press, New York, pp. 325-346.
- Badrian, N.L. & Malenky, R.K. (1984). Feeding ecology of *Pan paniscus* in the Lomako Forest, Zaire. In Susman, R.L. (ed.), *The pygmy chimpanzee: Evolutionary biology and behavior*, Plenum Press, New York, pp. 275-299.
- Boesch, C. & Boesch, H. (1989). Hunting behavior of wild chimpanzees in the Taï National Park. *Am. J. Phys. Anthropol.* 78: 547-573.
- De Waal, F.B.M. (1989). Food sharing and reciprocal obligations among chimpanzees. *J. Hum. Evol.* 18: 433-459.
- Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* 1: 161-331.
- Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Harvard University Press, Cambridge, MA.
- Hiraiwa-Hasegawa, M. (1990). Role of food sharing between mother and infant in the ontogeny of feeding behavior. In Nishida, T. (ed.), *The chimpanzees of the Mahale mountains*, University of Tokyo Press, Tokyo, pp. 27-275.
- Kano, T. (1980). Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *J. Hum. Evol.* 9: 243-260.
- Kano, T. (1982). The social group of pygmy chimpanzees *Pan paniscus* of Wamba. *Primates* 23: 171-188.
- Kitamura, K. (1983). Pygmy chimpanzee association patterns in ranging. *Primates* 24: 1-12.
- Kuroda, S. (1979). The social group of the pygmy chimpanzee. *Primates* 20: 161-183.
- Kuroda, S. (1980). Social behavior of the pygmy chimpanzee. *Primates* 21: 181-197.

- Kuroda, S. (1984). Interactions over food among pygmy chimpanzees. In Susman, R.L. (ed.), *The pygmy chimpanzee: Evolutionary biology and behavior*, Plenum Press, New York, pp. 301-324.
- McGrew, W.C. (1975). Patterns of plant food sharing by wild chimpanzees. In Kawai, M., Kondo, S. & Ehara, A. (eds.), *Contemporary primatology*, Karger, Basel, pp. 304-309.
- Moore, J. (1984). The evolution of reciprocal sharing. *Ethol. Sociobiol.* 5: 5-14.
- Nishida, T. (1970). Social behavior and relationship among wild chimpanzees of the Mahali Mountains. *Primates* 11: 47-48.
- Silk, J. (1978). Patterns of food sharing among mother and infant chimpanzees at Gombe National Park, Tanzania. *Folia Primatol.* 29: 129-141.
- Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*, 2nd ed. Freeman, New York.
- Teleki, G. (1973). *The predatory behavior of wild chimpanzees*. Bucknell, Pennsylvania, University Press.
- Thompson-Handler, N., Malenky, R.K. & Badrian, N. (1984). Sexual behavior of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaire. In Susman, R.L. (ed.), *The pygmy chimpanzee: Evolutionary biology and behavior*, New York, Plenum Press, pp. 347-368.
- Trivers, R.L. (1971). The evolution of reciprocal altruism. *Q. Rev. Biol.* 46: 35-57.
- White, F.J. (1988). Party composition and dynamics in *Pan paniscus*. *Int. J. Primatol.* 9: 179-193.
- White, F.J. (1989). Ecological correlates of pygmy chimpanzee social structure. In Standen, V. & Foley, R.A. (eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals*, Blackwell Scientific Publications, Oxford, pp. 151-164.
- White, F.J. (1992a). Pygmy chimpanzee social organization: Variation with party size and between study sites. *Am. J. Primatol.* 26: 203-214.
- White, F.J. (1992b). Activity budgets, feeding behavior and habitat use of pygmy chimpanzees at Lomako, Zaire. *Am. J. Primatol.* 26: 215-223.
- Wrangham, R.W. (1975). *The behavioural ecology of chimpanzees in Gombe National Park*. Ph. D. thesis, University of Cambridge.