# Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study

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REVIEW ARTICLE

# Factors underlying party size differences between chimpanzees and bonobos: a review and hypotheses for future study

**Takeshi Furuichi**

**Abstract** Differences in party size and cohesiveness among females have been primary topics in socio-ecological comparisons of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*). This paper aims to review previous studies that attempted to explain these differences and propose some hypotheses to be tested in future studies. Comparisons of recent data show that relative party size (expressed as a percentage of total group size) is significantly larger for bonobos than chimpanzees. Although the prolonged estrus of females, close association between mother and adult sons, female social relationships including unique homosexual behavior, and high female social status might be related to the increased party size and female cohesiveness of bonobos, these social and behavioral factors alone do not appear to explain the differences between the two species. Differences in ecological factors, including fruit-patch size, density of terrestrial herbs, and the availability of scattered foods that animals forage as they travel between large fruit patches could also contribute to the differences between chimpanzees and bonobos. However, these factors cannot fully account for the increased party size and female cohesiveness of bonobos. The higher female cohesiveness in bonobos may be explained by socio-ecological systems that reduce the cost in feeding efficiency incurred by attending mixed-sex parties. These systems may include female initiatives for party ranging movements as well as the factors mentioned above. Because of their geographical isolation, the two species probably evolved different social systems. Chimpanzees, whose habitats became very dry during some periods in the Pleistocene, likely evolved more flexible fission–fusion social systems to cope with seasonal and annual variation in food availability. On the other hand, bonobos had a large refugia forest in the middle of their range even during the driest periods in the Pleistocene. Therefore bonobos, whose habitats had more abundant food and smaller variation in food availability, probably evolved systems that help females stay in mixed parties without incurring large costs from contest and scramble competition.

**Keywords** Bonobo · Chimpanzee · Party size · Fission–fusion grouping · Female cohesiveness · Refugia forest

## Introduction

Along with the unique characteristics of prolonged estrus and homosexual behavior observed in bonobos (*Pan paniscus*) (Savage-Rumbaugh and Wilkerson 1978; Kuroda, 1980; Thompson-Handler et al. 1984; Furuichi, 1987; Kano, 1992), much attention has been paid to party size differences between this species and chimpanzees (*Pan troglodytes*) (Kuroda 1979; Kano 1982; Chapman et al. 1994b; Boesch 1996; Wrangham 2000; Hohmann and Fruth 2002; Mulavwa et al. 2008; Furuichi et al. 2008). Kuroda (1979) reported that the average size of a temporary bonobo aggregation party was 16.9 animals, much larger than the reported average party size for chimpanzees (see next section for details). Compared with chimpanzees, female bonobos exhibited a higher ratio of attendance in mixed-sex parties, and such female cohesiveness has sometimes been discussed with reference to their prolonged estrus and close social bonding with males and

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other females (Kuroda 1979, 1980; Kano 1982; Badrian and Badrian 1984; Furuichi 1987, 1989; White 1988). However, these factors alone could not explain the increased party size and female cohesiveness of bonobos relative to chimpanzees.

With progress in the ecological study of great apes, attempts have been made to explain differences in party size and female cohesiveness using environmental factors such as fruit-patch size, abundance of terrestrial herbaceous vegetation (THV), and presence of "feed-as-you-go" foods (small foods that animals can feed on while traveling between large food patches) (White and Wrangham 1988; Malenky and Stiles 1991; Kano 1992; Chapman et al. 1994a, b; Malenky and Wrangham 1994; Wrangham et al. 1996; White 1998; Wrangham 2000). Boesch (1996) pointed out that both party size and grouping patterns of chimpanzees in Taï, Côte d'Ivoire, were similar to those of bonobos inhabiting similar rainforest study sites. His claim encouraged us to hypothesize that party size differences were not strictly due to species differences but were also influenced by environmental differences between the moist evergreen forests inhabited by most of studied bonobo populations the drier semideciduous forests inhabited by most of studied chimpanzee populations. In this context, studies at Lukuru in the Democratic Republic of Congo (DR Congo), a drier at the southern limit of the bonobo range characterized by patchy riverine forest and savanna, received much attention (Myers Thompson 2001, 2002, 2003). Do bonobos living in this area exhibit grouping patterns more similar to those of chimpanzees in similar habitats? Unfortunately, political unrest in the DR Congo closed all bonobo study sites by 1996, and comparative studies relating to grouping patterns and the environment were possible only for gorillas and chimpanzees.

Bonobo studies subsequently resumed in and around the Salonga National Park, DR Congo (Hohmann and Fruth 2003; Grossmann et al. 2008; Mohneke and Fruth 2008; Reinartz et al. 2008) and Hohman and colleagues in particular began systematic ecological studies of bonobos at Lui Kotale (Hohmann and Fruth 2003). At Wamba in the northern sector of the Luo Scientific Reserve, DR Congo, ecological studies of bonobos resumed in 2002 (Furuichi and Mwanza 2003; Idani et al. 2008). Prior to 1996, researchers used artificial provisioning at Wamba to facilitate close observation of bonobo social behavior. However, because of increased recognition of the risk of disease transmission between humans and animals, studies in the past 12 years have not employed artificial provisioning. Ecological studies also resumed at Lomako, DR Congo, in 2005 and have been carried out continually since 2007 (White et al. 2008). Thus valuable data on the ecology of bonobos under natural conditions are being obtained at all three representative study sites (Hohmann

et al. 2006; Furuichi et al. 2008; Mulavwa et al. 2008; Waller et al. 2008). These studies basically reconfirmed the results of previous ecological studies of bonobos. Research at Lui Kotale (Hohmann et al. 2006) and Wamba (Mulavwa et al. 2008) confirmed that party size was larger for bonobos than for chimpanzees and did not differ significantly between natural conditions and the previously reported artificial provisioning at Wamba. Furthermore, the two study sites provided valuable information on the relationship between party size and seasonal changes in fruit food production.

In spite of all these efforts, however, no single hypothesis regarding social or ecological factors appears to explain clearly the party size difference between chimpanzees and bonobos, although most of the factors that have been proposed seem partly responsible. This paper will review reports on the party size of chimpanzees and bonobos, review proposed social and ecological hypotheses on the party size difference, and propose some hypotheses to be tested in future studies to obtain a more comprehensive view of differences in socio-ecological systems between the two species.

## Party size differences

Chimpanzees and bonobos tend to form male-philopatric groups (Nishida 1979; Kano 1982; Nishida et al. 2003; Hashimoto et al. 2008), also known as unit groups or communities (Van Elsacker et al. 1995), which consist of flexible ranging parties (Nishida 1979; Kano 1982; Goodall 1986; White 1988; Furuichi 2006). The formation of temporary parties is believed to be a foraging behavior for adapting to seasonal changes in the distribution and abundance of fruit (Wrangham 1986; Wrangham et al. 1993; Chapman and Chapman 2000; Lehmann et al. 2007). Consequently, party size differences within and between species have been a primary focus of ecological studies on *Pan* spp. However, different methodologies employed at different study sites have made intra- and interspecies party size comparisons difficult (Chapman et al. 1993, 1994b; Hashimoto et al. 2001). Various studies have estimated party sizes by scanning sampling (White 1988; Wrangham et al. 1992; face-to-face party in Itoh and Nishida 2007) or by the number of animals observed per hour (Chapman et al. 1995; Doran 1997; Hashimoto et al. 2001), per day (Boesch 1996; Matsumoto-Oda 1999; nomadic party in Itoh and Nishida 2007) or per some unspecified time period (Kuroda 1979; Sakura 1994).

Despite these different methods, mean party sizes for bonobos tend to be larger than those for chimpanzees. If we exclude data that incorporate observations at permanent provisioning sites (Nishida 1968 for Mahale, Kano 1982

**Table 1** Comparison of absolute party size and relative party size (or attendance ratio) of chimpanzees and bonobos

| Study site | Absolute party size | | | | Relative party size | | | |
|---|---|---|---|---|---|---|---|---|
| | All individuals | Independent individuals | | | Independent individuals | | | |
| | All | All | Male | Female | All | Male | Female | |
| Chimpanzee | | | | | | | | |
| Bossou | 4.0 | | | | 20 | | | Sakura (1994) |
| Taï | 8.3 | | | | 11 | | | Boesch (1996) |
| Taï | 10.0 | | | | 13 | | | Boesch and Boesch-Achermann (2000) |
| Gombe | 5.6 | | | | 9 | | | van Lawick-Goodall (1968) |
| Mahale[a] | 8.1 | 6.2 | | | 30 | | | Nishida (1968) |
| Mahale | | 4.0 | | | 13 | | | Face-to-face part in Itoh and Nishida (2007) |
| Kanyawara | | 5.6, 6.1 | | | 13 | | | Wrangham et al. (1992) |
| Kanyawara | | 5.11 | | | | | | Chapman et al. (1994a, b) |
| Ngogo | | 5.0 | | | | | | Wrangham et al. (1992) |
| Ngogo | | 10.3 | | | 9 | | | Mitani et al. (2002) |
| Budongo | | 5.0 | | | 19 | | | Reynolds (2005) |
| Kalinzu | | 5.9 | 3.5 | 1.2 | 13 | 20 | 6 | Mulavwa et al. (2008) |
| Bonobo | | | | | | | | |
| Wamba | 16.9 | | | | 29 | | | Kuroda (1979) |
| Wamba[a] | 18.9 | 14 | 7.2 | 6.8 | 30 | 36 | 28 | Kano (1982) |
| Wamba[a] | 22.7 | | | | | | | Idani (1991) |
| Wamba | 11.2 | 8.7 | 4.1 | 3.2 | 51 | 41 | 53 | Mulavwa et al. (2008) |
| Lomako | | 7.9 | | | | | | Badrian and Badrian (1984) |
| Lomako | | 6.2 | | | | | | White (1988) |
| Lomako | | 5.4 | | | | | | Malenky and Stiles (1991) |
| Lomako | | 7.2, 7.3 | | | | | | White (1996) |
| Lomako | | 4.9 | | | 27 | | | Hohmann and Fruth (2002) |
| Yalosidi | 8.5 | | | | | | | Kano (1983) |

Table expanded upon from Hohmann and Fruth (2002)

[a] Data incorporating observations at permanent provisioning sites

and Idani 1991 for Wamba), the number of independent individuals ranges from 4.0 to 10.3 for chimpanzees and from 4.9 to 8.7 for bonobos; when all animals are considered, the number ranges from 4.0 to 10.0 for chimpanzees and from 8.5 to 16.9 for bonobos (Table 1). However, the within-species variation is considerably larger than the interspecies variation. Converting absolute party size for independent individuals to party size for all individuals using the all individual/independent individual ratio of 1.31 for chimpanzees (Nishida 1968) and 1.32 for bonobos (average of Kano 1982 and Mulavwa et al. 2008), and using an average value for each study site as an independent sample, the difference between chimpanzees and bonobos is only a trend (Mann–Whitney, $n1 = 8$, $n2 = 3$, $U = 4.0$, $P = 0.10$). Boesch (1996) suggested that mean party size should be expressed as a percentage of the total group size, because a party of 10 animals might have a different socio-ecological significance in a group of 30 animals than in a

group of 100 animals. Using this convention, party size differences between chimpanzees and bonobos are more conspicuous, with nonoverlapping ranges of 9–20% for the chimpanzees and 27–51% for the bonobos (excluding data that incorporates observations at provisioning sites). The statistical test using the average value for each study site as an independent sample showed that the between-species difference is significant (Mann–Whitney, $n1 = 8$, $n2 = 2$, $U = 0.0$, $P < 0.05$). These results suggest that bonobos form more cohesive groups than do chimpanzees.

Higher female cohesiveness in bonobos may be a key factor leading to larger party size. At Wamba, females exhibited a higher attendance ratio in parties under artificial provisioning conditions (Furuichi 1987; Kano 1992). Recent studies under natural conditions have shown that the attendance ratio of females always exceeds that of males irrespective of the party size (Fig. 1a, Furuichi et al. 2008; Mulavwa et al. 2008). At Lomako, the greatest level
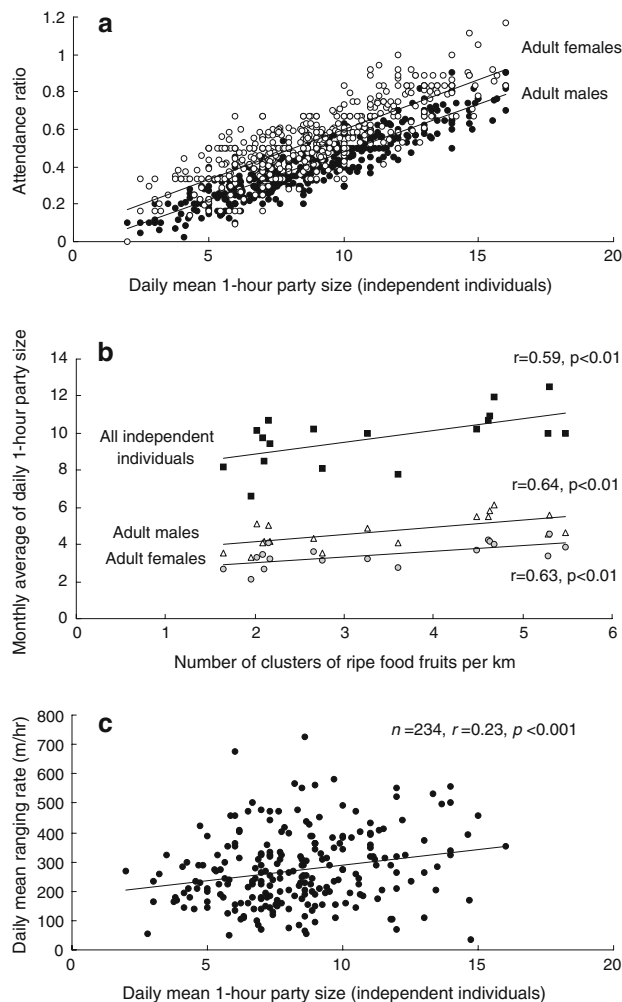
Fig. 1 Relationships of **a** attendance ratio of males and females with party size, **b** party size with fruit abundance, and **c** ranging rate with party size. Figures cited from Mulavwa et al. (2008) and Furuichi et al. (2008); see those papers for more details

of cohesiveness was found between females, although the party size was smaller than at Wamba (White 1988). A comparison of the relative party size of males and females between chimpanzees in the Kalinzu Forest (Uganda) and bonobos at Wamba clearly demonstrates the higher cohesiveness of females in bonobos (Table 1). Kuroda (1980) reported that the relative affinity index between bonobos based on grooming frequency was highest between males and females (100), second between females (81), and lowest between males (42). These indices were very different from those for chimpanzees in Mahale, where the index was highest between males (100), second between males and females (17), and lowest between females (5). The relatively strong social bonds observed between males and females in bonobos and between females seemed to be related to the larger party sizes observed for bonobos relative to chimpanzees.

## Social factors

### Enhanced male–female bonding

With the unusual tendency of female bonobos to exhibit pseudo-estrus during nonconceptive periods, one might suppose that a longer estrous period could lead to stronger social bonds between males and females and contribute to the formation of larger parties. In fact, chimpanzee parties including estrous females tend to be larger regardless of fruit availability (Nishida 1979; Goodall 1986; Hashimoto et al. 2001). Kano (1982) reported that, in bonobos, 96% of the observed parties were mixed sex, and 98% included at least one estrous female. Furuichi and Hashimoto (2002) also reported that three or four females exhibited estrus simultaneously in bonobos. Therefore, if estrous females attend mixed parties more frequently than anestrous females and attract more males to these parties, the prolonged estrus of bonobos could be directly responsible for the larger party sizes of bonobos relative to chimpanzees. However, some studies showed that estrus influenced neither estrous females' attendance at mixed parties nor their association patterns (Furuichi 1987; Furuichi and Hashimoto 2002). Additionally, per-hour copulation rate was lower for bonobo females than for chimpanzee females, and neither bonobo males nor estrous females exhibited sexual behaviors as excitatory as their chimpanzee counterparts (Furuichi 1997; Furuichi and Hashimoto 2002, 2004; Hashimoto and Furuichi 2006). Therefore, it is not clear to what extent the prolonged estrus of female bonobos contributes to the larger party size of bonobos relative to that of chimpanzees.

In studies making use of improved individual identification and knowledge about personal life histories, it appears that the strongest social bonds in bonobos at Wamba were those between mothers and their adult sons. Kano (1982) reported that males tended to be in the same party as their mothers throughout adolescence and even during adulthood. Furuichi (1989) showed that the frequency of staying within 3 m was highest for mothers and their adult sons. These strong associations served as important social units, and the dominance status of adult males was sometimes influenced by the supportive behaviors of their mothers (Kano 1992; Furuichi and Ihobe 1994; Furuichi 1997). Thus, a large proportion of male–female bonding in bonobos was not related to sexual attraction, but instead to the relationship between mothers and adult sons. Such mother–son relationships could contribute to the formation of larger bonobo parties if male bonobos tend to range together as do male chimpanzees, and females prefer to stay with their sons rather than range alone or in small parties of females. However, the reason for the extended mother–son association period is not yet understood.

## Close association among females

As stated above, the second closest social association in bonobos is between females. It is curious that female–female association is stronger than male–male association in bonobos because both bonobos and chimpanzees form male-philopatric groups. Are the closer female–female social relationships observed in bonobos responsible for the increased female cohesiveness and party size relative to chimpanzees?

Young immigrant female bonobos tend to exhibit very positive behaviors directed toward establishing close social relationships with specific senior females (Furuichi 1989; Idani 1991). These behaviors include approaching their elders, begging for food from them, and soliciting genito-genital rubbing. Thus, female bonobo associations are not merely for aggregation but appear to be based on specific interindividual relationships. Such close interindividual associations could contribute to the female attendance in mixed parties. Although adult females are usually immigrants from other groups (Furuichi 1989; Kano 1992; Gerloff et al. 1999; Hohmann et al. 1999; Eriksson et al. 2006; Hashimoto et al. 2008), female aggregates typically occupy central positions of mixed parties, and individual females sometimes ally with one another in agonistic interactions with adult males (White and Lanjouw 1992; Parish 1994; Hohmann and Fruth 1996; Furuichi 1997; Vervaecke et al. 2000; White and Wood 2007). Based on these tendencies, one could argue that the high cohesiveness of female bonobos could be the result of these strong interindividual associations and the unique socio-sexual behaviors that facilitate it. However, one could equally argue that female bonobos developed strong interindividual associations and socio-sexual behaviors to cooperate effectively with unrelated females during times when female aggregation was necessary for survival (Wrangham 1993). Thus, the causal relationships between close female–female interindividual associations and female cohesiveness remain unclear.

## High social status of females

The high social status of females could also be related to the increased female cohesiveness and party size of bonobos relative to chimpanzees. Despite some uncertainty regarding the overall dominance of male and female bonobos, the high social status of females is clearly a unique characteristic of bonobos relative to the other great apes that exhibit male-dominant societies (Parish 1994, 1996; Kano 1992; Furuichi 1997; Paoli and Palagi 2008; Stevens et al. 2007, 2008; White and Wood 2007). It appears that male and female bonobos share equal dominant status in the wild, while females are frequently dominant over males in captivity. Furuichi (1997) and White and Wood (2007) reported that wild females tended to behave dominantly toward males where food was concerned, and this might explain female dominance in captivity where competition over food is more explicit.

If female bonobos dominate males in feeding situations, their high social status could reduce the competitive costs for females and facilitate their attendance in mixed parties. However, even in chimpanzees, aggressive interactions with males and displacements by males from food do not seem to prevent females from attending parties, though this trend is not confirmed by quantitative data (Goodall 1986; Wrangham 2000). If contest competition is not a primary factor for the relatively low cohesiveness of female chimpanzees, the relatively high social status of female bonobos is not likely a primary cause for the high cohesiveness of female bonobos.

## Ecological factors

### General model for chimpanzees

Early studies of chimpanzees and bonobos mainly focused on behavioral traits for comparison with their human relatives. However, as the number of chimpanzee and chimpanzee–gorilla study sites increased in the 1980s, the ecologies of these species came to attract more attention. Researchers investigating different species and sites attempted to establish a unified methodology to assess the abundance and distribution of food so that their results could be more directly compared (e.g., Malenky et al. 1993, 1994; Chapman et al. 1994a). Many ecological and environmental hypotheses were presented and tested to explain the party size and composition of chimpanzees and bonobos (e.g., Wrangham 1986; White and Wrangham 1988; Chapman et al. 1994b; Malenky et al. 1994).

A general model based on the abundance and distribution of food, party size, and attendance of males and females to the party was established for chimpanzees (Wrangham 1979a, b, 1987, 2000; Terborgh and Jaonson 1986; Pusey and Packer 1987; Chapman and Wrangham 1993; Chapman et al. 1994b, 1995; Janson and Goldsmith 1995; Bean 1999; Furuichi 2006). Because fruit, the primary food of *Pan* species, is limited in a given patch, it is consumed faster by larger than smaller foraging parties, necessitating more frequent movements of larger parties between different patches. Females, especially those with dependent offspring, are likely to incur a heavier cost from more frequent movements because they are slower and spend more time moving between patches than males. Females tend to be more stationary and efficient feeders than males, who may sacrifice feeding efficiency for

increased ranging of wider areas in search of estrous females and to settle territorial concerns. Therefore, chimpanzees split into smaller parties when large fruit patches are not available, and females are more likely to range alone or in small parties than to attend large parties.

## Food patch size

Based on this general hypothesis, researchers have studied the size and distribution of food patches in *Pan* habitats to determine whether larger food patches reduce feeding competition and contribute to the larger party size of bonobos. White and Wrangham (1988) performed a systematic comparison of fruit-patch sizes at different sites for chimpanzees (Gombe, Tanzania) and bonobos (Lomako). They reported that bonobos exhibited larger party sizes and used larger fruit patches than chimpanzees. However, their use of feeding time to measure fruit-patch size did not represent the amount of available fruit, but only the amount of fruit consumed in a patch. On the other hand, Chapman et al. (1994b) compared the actual fruit-patch sizes used by chimpanzees at Kibale, Uganda, and bonobos at Lomako. Although they employed tree diameter at breast height at Kibale and tree crown diameter at Lomako for patch measurements and only single populations were compared, these authors suggested that fruit-patch size could not explain party size differences between chimpanzees and bonobos.

Terrestrial herbaceous vegetation (THV) has been another key factor considered in comparisons between chimpanzee and bonobo study sites because it usually exists as large food patches. Badrian and Malenky (1984) reported that, following their favorite food of fruit, the piths of seven different THV species, including the most frequently eaten *Haumania liebrechtsiana*, constituted the second favorite food source of bonobos at Lomako. THV was also used by bonobos at other study sites including Wamba (Kano and Mulavwa 1984) and Yalosidi in DR Congo (Kano 1983). Malenky et al. (1994) and Malenky and Wrangham (1994) confirmed that the density of THV was higher for bonobos in Lomako, and that Lomako bonobos consumed more THV than did chimpanzees in Kibale.

However, the potential contribution of THV to party size is neither identical nor easy to interpret for these two species. Malenky and Wrangham (1994) suggested that the use of THV differed between the two species, such that Lomako bonobos consumed protein-rich THV as a protein source regardless of season or fruit abundance, whereas Kibale chimpanzees consumed carbohydrate-rich THV as a fallback carbohydrate source (protein: 30.6% of dry weight of THV in Lomako versus 9.3% in Kibale; water-soluble carbohydrate: 1.6% in Lomako versus 9.8% in Kibale).

Furthermore, the availability and use of THV varied among different chimpanzee sites as exemplified by its relative nonuse as a fallback food source at Lopé, Gabon, even when fruit was in scarce supply (Tutin et al. 1997), and its use as a non-fallback source in Kalinzu (Furuichi et al. 2001). Furuichi et al. (1997) showed that the abundance of THV could not explain the difference in chimpanzee density between sites with scarce THV, such as at Petit Loango, Gabon, and many other sites with abundant THV. Therefore, although the abundance and use of THV probably contribute somewhat to party sizes in general, THV did not specifically provide an obvious explanation for the greater party sizes of bonobos relative to chimpanzees.

## Feed-as-you-go foraging

Wrangham (2000) proposed another hypothesis, namely that feed-as-you-go foraging may explain the larger party size in bonobos. He supposed that bonobos forage as they travel between fruit patches because their environment provides abundant high-quality (protein-rich) THV, and therefore parties travel at a lower velocity than nonforaging females would on a journey between fruit patches. In fact, while following the ranging movement of bonobos at Wamba, we very frequently encountered remains of foods that they ate as they traveled. Those foods included not only THV but also fruits and young leaves of small dispersed trees. The frequency of encounters with such feed-as-you-go foods among bonobos at Wamba was much higher than among chimpanzees in the Kalinzu Forest (Furuichi, unpublished data). The general model mentioned above predicts that females, especially those with dependent offspring, incur a large cost when ranging in large parties that frequently shift between discrete fruit patches. However, if parties travel slowly enough, females would be unlikely to incur disadvantages caused by longer ranging time or later arrival at new fruit patches. Thus, the abundance of foods for feed-as-you-go foraging might explain why female bonobos show higher attendance at parties, which may be responsible for the larger party size in bonobos relative to chimpanzees.

To examine this hypothesis, we need to compare the two species with regard to the velocity of individual males and females and that of mixed-sex parties when they travel between fruit patches. Although such comparable data are not currently available, estimated mean day range of the two species may provide some tentative insights. The mean day range for mixed parties in bonobos at Wamba was estimated to be 2.6 km (Furuichi et al. 2008). Though there are no comparable data for mixed parties in chimpanzees, the mean day ranges of individual chimpanzees in five groups (communities) in Kanyawara, Gombe, and Taï were between 2.1 and 4.6 km for males and between 2.0 and

4.1 km for adult females (Wrangham 1977; Pontzer and Wrangham 2004). Because males usually lead movements of mixed parties of chimpanzees, the day range of the mixed parties in chimpanzees may be equivalent to that of individual male chimpanzees, and therefore longer than that of mixed parties in bonobos. Thus, if chimpanzees and bonobos use same proportion of daytime for traveling, the velocity of the mixed parties traveling between fruit patches may be greater for chimpanzees. Additional data are needed for more explicit comparisons.

## Recent studies on the relationship between fruit production and party size

With the realization that food-patch size alone did not explain the increased party size and female cohesiveness of bonobos relative to chimpanzees, Chapman et al. (1994b) hypothesized that seasonal variations in level or intensity of feeding competition were responsible for these differences. They suggested that chimpanzees experienced greater variations in feeding competition than bonobos so that, for part of the year, the lack of large food patches prohibited female sociality and temporarily removed the advantage of female cohesiveness. Bonobos experienced fewer variations in feeding competition, thereby allowing females to remain gregarious throughout the entire year. By examining this hypothesis, White (1998) showed that no consistent seasonal variation in fruit abundance or diet existed for bonobos at Lomako, and that the increase in monthly fruit abundance was associated with a significant increase in the number of males in a party but not in the number of females. Hohmann and Fruth (2002) showed that the numbers of independent adult males or females in a bonobo party were not related to the abundance of fruit at Lomako.

Using data from a new bonobo study site at Lui Kotale, Hohmann and Fruth (2003) examined the seasonal changes of food production and nutritional content, and Hohmann et al. (2006) compared these results with those for chimpanzees at Gashaka, Nigeria. While the large climatic and vegetation differences between these two sites caused some concerns for interpretation, significantly different relationships between the monthly fruit production and nest group size, which represents party size, were found between the two species: chimpanzees, but not bonobos, exhibited a significant positive correlation between nest group size and fruit production.

The studies at Wamba resumed in 2002 and contributed more details concerning the relationships between fruit production, ranging rate, and party size and composition (Furuichi et al. 2008; Mulavwa et al. 2008). The data from 484 observation days over 30 months established that fruit production was seasonal, and the mean monthly party size was significantly correlated with the mean monthly fruit production (Fig. 1b). The mean daily ranging rate, representative of the daily ranging distance (day range), exhibited a large variance but was significantly correlated with the mean daily party size (Fig. 1c). These positive correlations were compatible with the general model proposed for chimpanzees. However, although significant, the seasonal variations in the party size and ranging rate were very limited. The expected number of independent individuals differed only by 1.5 males and 1.1 females between the highest fruiting month and the lowest fruiting month, and the expected mean daily ranging rate increased by only 10.6 m/h with the addition of one individual (Furuichi et al. 2008). Therefore, the results for the Wamba bonobos differ very little from the results for the Lomako and Lui Kotal bonobos, where party size was independent of fruit availability.

The significant correlation of small substantial changes between party size and fruit production for the Wamba bonobos reminded us of an important difference between reports on chimpanzees and bonobos: the relationship between fruit production and party size is more variable among reports on chimpanzees than among those on bonobos. Although the general model for chimpanzees predicted a positive correlation between fruit abundance and party size, studies from different chimpanzee sites have reported contradictory results. Some studies showed that chimpanzees formed larger parties during seasons with higher fruit abundance, as predicted by the model (Wrangham 1977; Ghiglieri 1984; Isabirye-Basuta 1988; Boesch 1996; Matsumoto-Oda et al. 1998; Itoh and Nishida 2007). However, other studies reported that chimpanzee party size was greatest in the dry season when food was restricted at Gombe (Stanford et al. 1994), that no positive relationship between fruit abundance and party size existed at Kahuzi-Biega, DR Congo (Basabose 2004), and that neither monthly party size nor the number of adult anestrous females per party was related to the abundance of any fruit categories in Budongo, Uganda (Newton-Fisher et al. 2000; Wakefield 2008). The positive relationship between fruit abundance and party size did not hold when multiple sources of important foods were available at Kibale (Isabirye-Basuta 1988), and the relationship between fruit abundance and party size likely displayed marked differences over the years at Taï (Boesch 1996).

Hashimoto et al. (2001) reported that, for the chimpanzees at Kalinzu, fruit abundance did not significantly influence party size, but the presence or number of estrous females did. In fact, previous studies showed that the presence or number of estrous females had a large impact on the grouping of chimpanzees (e.g., Nishida 1979;

Goodall 1986). This could partly explain why the relationship between party size and fruit abundance is so different among the many reports reviewed above. If female estrus occurred during the low fruiting season by coincidence in a given year, the effect of estrous females could mask a significant correlation between party size and fruit abundance in that year (Boesch 1996). In bonobos, at least one female in a group was in estrus at any given time (Kano 1982; Furuichi and Hashimoto 2002), so the presence of estrous females did not serve as a main factor for party size. This could explain why a significant correlation was found between party size and fruit abundance in bonobos at Wamba, even though the actual change in the party size was very small (Fig. 1b).

## Hypotheses to be examined in future studies

### Why do females aggregate more than males?

The relative party size, or attendance ratio, of individual members in Table 1 and Fig. 1a shows a robust difference between chimpanzees and bonobos: the attendance ratio of females is higher than males in bonobos while it is lower than males in chimpanzees (Wrangham 1979, 2000; Kano 1982; Furuichi 1987; White 1988; Furuichi et al. 2008; Mulavwa et al. 2008). One may question whether the factors examined above explain the opposing tendencies of male and female attendance. Ecological factors alone do not appear to explain this difference. Chimpanzees inhabit a wide variety of habitats that vary from rainforest in Côte d'Ivoire to semi-arid areas in Senegal and Tanzania, and the habitats of bonobos may be included within this range of variation. In fact, at Taï, where habitat type is similar to the major habitat type of bonobos, chimpanzees show more cohesive grouping patterns than do chimpanzees in other drier habitat, but males still have a stronger tendency than females to attend mixed parties (Doran 1997; Boesch and Boesch-Achermann 2000). Thus, to understand the reversed tendency for aggregation between males and females, we may need to consider both ecological and social factors.

The model illustrated in Fig. 2 might offer an explanation for these opposing tendencies for aggregation between sexes. For simplicity, let us tentatively consider that males of both chimpanzees and bonobos show a similar tendency for aggregation (line I). As the cost for feeding incurred by attending a party increases due to the food distribution and ranging pattern, the frequency of attending a party will decrease. This decrease may be slow initially because males may receive some social benefit by continuing the association (such as alliances for obtaining higher social rank within the group or to protect territory from other
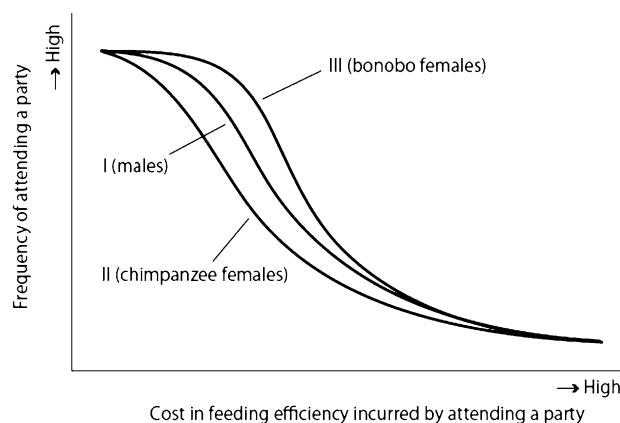


**Fig. 2** A model of changes in the cohesiveness of males and females in relation to the increase in the cost in feeding efficiency incurred by attending a party

groups), but eventually the attendance ratio decreases when the cost in terms of feeding efficiency overcomes the benefit from maintaining the association. In most group-living mammals, females tend to aggregate more than males. Aggregated females are more likely to avoid predation, retain the support of their relatives or peers, and share information about geography, predators, and food (e.g., Pusey and Packer 1987). However, if there is little benefit from maintaining an association, because of a lack of kin relations among females or serious risk of predation, and if the cost for feeding in parties is greater for females due to their lower mobility and subordinate social status, the frequency of attending parties may decrease more rapidly for females than for males (line II). This may explain the lower tendency for aggregation among female chimpanzees. By contrast, if females can develop some social mechanism to moderate the cost imposed by ranging in parties, they might be able to sustain a higher attendance ratio than males to maintain the benefits of aggregation mentioned above, until the feeding cost increases to a certain level (line III). This may represent the condition for female bonobos. Thus, in habitats in which the cost to feeding efficiency is not very high when ranging in parties, female bonobos aggregate more than males, whereas female chimpanzees disperse more than males do.

As mentioned in the section on social factors, high social status itself may reduce the cost of contest competition for females that join mixed parties. In bonobos, the unique genito-genital rubbing behavior between females and the tendency of immigrant females to form close social relationships with specific senior females may help the formation and maintenance of close associations among females, which may facilitate the formation of alliances to combat harassment by males and protect priority of access to food resources. Furthermore, female bonobos frequently control the ranging movements of mixed parties, probably

because of their high social status, but also because older adult females greatly influence the behavior of their adult sons due to the strong lifelong bond between mothers and sons.

At Wamba, party movements typically occurred when members descended from a tall fruit tree and took a short break on lower trees while watching one another. Some of the males climbed down and performed branch-dragging behavior while running on the ground to propose a direction of movement. However, the entire party did not move until the dominant females climbed down and initiated movement in a direction of their own choice (Furuichi, unpublished observation). A mixed party usually ranged in one area for up to several weeks and then shifted to another area. While restricted to a particular area, the day range was similarly restricted to shorter distances. Even when males explored greater distances, seemingly to shift to another area, they usually abandoned these attempts if the females did not follow and returned to the original area to join the females by the evening (Furuichi et al. 2008).

It has been shown that male chimpanzees move more quickly between food patches (dissertation of Hunt cited in Wrangham 2000) and over a longer distance daily (Wrangham 1977; Pontzer and Wrangham 2004) than do female chimpanzees. Therefore, if females join a mixed party whose movement is controlled by males, they may incur the greater cost of scramble competition with males due to their lower mobility. However, if females control the movement of mixed parties, the ranging rate would not exceed a level acceptable to females, and females attending mixed parties could thus lower the cost of scramble competition.

Reconsideration of the difference in grouping patterns

Another question may arise from the above hypothesis: why have female bonobos developed a social system that moderates the costs in feeding efficiency incurred by attending mixed parties while female chimpanzees have not? To answer this question, we may need to reconsider the differences in the grouping patterns of chimpanzees and bonobos, taking into account historical differences in the environment and evolutionary processes.

Although many authors have stated that both chimpanzees and bonobos have a fission–fusion social structure, the nature of the fission–fusion may differ between the two species. Chimpanzees tend to form temporary parties that change in membership very flexibly. If we start following a party in the morning, the membership will change several times before the evening. Many parties may range in a certain area while communicating through vocalizations, but some parties or lone females may range and sleep at night in distant areas. Matsumoto-Oda et al. (1998) defined

the party size as the number of animals confirmed in 1-day observations while following focal animal(s) in Mahale. This party size is much larger than the temporary party sizes that are listed in Table 1 (12.7 independent animals), but is still only 30% of the total group members.

Bonobos also form flexible parties during the daytime. However, most of them usually range in the same area while exchanging their vocalizations, and they tend to aggregate in one area toward the evening (Kano 1982; Furuichi 1987). Although they sometimes sleep at two or more nesting sites, they are quite close to each other and often join the same mixed party the following morning. In the study period from 1985 to 1986, 89% of adult and adolescent females were confirmed in 1-day observations as we followed a mixed party (Furuichi 1987).

These differences are apparent when we compare the charts in the early studies of chimpanzees (Nishida 1968) and bonobos (Kano 1982). Whereas chimpanzees showed frequent and flexible fission–fusion of parties, bonobos divided less frequently into fewer parties, and the memberships of the parties were stable for longer periods. The same tendency for bonobos was also found in recent studies, 12 years after the cessation of artificial provisioning. During a 2-month study period starting in August 2007, nearly all members of the study group were observed at least once every day as we followed a mixed party, suggesting that no long-lasting splits into plural parties occurred. During the next study period starting in January 2008, in the season with the lowest fruit availability, splitting into a few separate parties was sometimes observed. However, unlike for chimpanzees, the membership of each party of bonobos was quite stable until they merged again into one party after a few days (Sakamaki and Furuichi, unpublished data). Sakamaki proposed that a substantial difference exists between the fission–fusion grouping of chimpanzees and that of bonobos, and that the lack or low frequency of fission–fusion among bonobos also explains the smaller variety of greeting behaviors (Furuichi and Ihobe 1994) and lower frequency of mutual grooming in bonobos.

Since the two species have been geographically isolated by the Congo River (Myers Thompson 2003), chimpanzees and bonobos may have undergone different trends in the evolution of socio-ecological systems. Chimpanzees, whose habitats on the right bank of the Congo River became very dry during some periods in the Pleistocene (Mayr and Ohara 1986; Plana 2004), may have developed highly flexible fission–fusion social systems to cope with seasonal and annual variation in the abundance and distribution of fruits. On the other hand, the area on the left bank had a large central refugia forest even during the driest periods, and the habitats of bonobos might have had relatively larger fruit patches, higher density of foods, and

smaller seasonal and annual variation in food availability. Under such circumstances, bonobos may not have experienced the necessity for such highly flexible fission–fusion grouping, and therefore may have developed social systems that help unrelated females to stay in mixed parties without incurring large costs from contest and scramble competition. These systems may include the prolonged estrous period in females, close mother–son social relationships, genito-genital rubbing and other social behaviors between females, dominance status in females equivalent to that in males, and female initiative in the ranging movements of parties. Once such features were established, female bonobos may have been able to retain their cohesiveness even in drier habitats similar to those in which female chimpanzees range alone or in smaller parties to maintain feeding efficiency.

If this hypothesis holds, the differences in the grouping patterns and especially in female cohesiveness between chimpanzees and bonobos may be substantial differences that have formed through the long process of ecological and behavioral adaptation to the habitats of each species (Wrangham 1993; Furuichi 2006), rather than reflecting merely current environmental differences. This hypothesis may be tested by comparing grouping patterns of chimpanzees and bonobos living in similar habitats. As mentioned above, the difference in female cohesiveness between chimpanzees at Taï and bonobos at Wamba living in similarly dense forest habitats supports this idea (Doran 1997; Boesch and Boesch-Achermann 2000), and we expect to see the results of further comparisons between the populations of the two species living in drier habitats (Moore 1996; Myers Thompson 2001, 2002; Ogawa et al. 2007).

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