

# Seasonal Changes in Fruit Production and Party Size of Bonobos at Wamba

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## Introduction

Because chimpanzees (*Pan troglodytes*) have a unique fission-fusion social structure, many researchers have investigated the nature of foraging parties. They have reported that chimpanzees form foraging parties whose size and sex composition change flexibly, and that the sizes of parties may vary according to fluctuations in fruit abundance, the number of estrous females, or both (Wrangham 1977, Ghiglieri 1984, Isabyre-Basuta 1988, Stanford et al. 1994, Boesch 1996, Matsumoto-Oda et al. 1998, Newton-Fisher et al. 2000, Boesch and Boesch-Achermann 2000, Hashimoto et al. 2001). Researchers have also reported that females tend to join mixed-sex parties less frequently than males do, and that this likely occurs because ranging in large mixed-sex parties may not be beneficial to the feeding activities of females (Wrangham 1979, 2000, Janson and Goldsmith 1995, Williams et al. 2002, Reynolds 2005).

The closest relative of chimpanzees, bonobos (*P. paniscus*), have a similar fission-fusion social structure. However, the size and composition of the parties are different from those of chimpanzees. Previous studies of bonobos at Wamba and Lomako in the Democratic Republic of the Congo showed that bonobos form larger and more stable parties (Kuroda 1979, Kano 1982, 1992, Furuichi 1987, White 1988), and that the size of parties may be influenced by fruit abundance to a lesser extent. This is probably because either the seasonal changes in fruit abundance are small or because some foods are available year-round (Kano 1982, Kano and Mulavwa 1984, White 1998, Malenky and Stiles 1991, Malenky and Wrangham 1994, Chapman et al. 1994). Furthermore, bonobo females tend to join mixed-sex parties

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more frequently than males do (Kano 1982, Furuichi 1987, White 1988). Because chimpanzees and bonobos form male-philopatric groups, it is not surprising that in chimpanzees, kin-related males aggregate more than unrelated females. Even in Taï, Côte d'Ivoire, where the sex difference in sociality among chimpanzees is less than at other sites, the composition of mixed parties is consistently male-biased (Boesch 1996). However, with bonobos, unrelated females aggregate more than related males. Although the higher sociality of female bonobos may be attributable to their high social status, which reduces the cost of contest competition, or to the higher density of food resources in bonobo habitat, which reduces the cost of scramble competition for slower-moving females, the hypotheses have not been examined quantitatively.

Thus, the differences in party size, party composition, and especially the grouping pattern of females, are key issues in understanding the ecological adaptations of *Pan* species. However, many constraints are imposed in examining proposed hypotheses to explain the differences between chimpanzees and bonobos. First, unlike chimpanzees, very limited information is available on the relationship between fruit abundance and party size in bonobos. Kuroda (1979) suggested the possibility of a relationship between seasonal fruit abundance and party size, but his study did not present quantitative data on fruit abundance. Although White (1998) and Hohmann and Fruth (2002) at Lomako presented quantitative analyses on the relationship between fruit abundance and party size, quantitative studies on more populations of bonobos are needed to reveal the relationship between the ranging pattern and seasonal changes in fruit abundance. Second, although Chapman et al. (1994) compared party size and fruit abundance between chimpanzees and bonobos, they indicated that their results were provisional, because party sizes may vary due to differences in observation methods. In fact, various methods and definitions have been proposed and used for the study of chimpanzee party size, and the different methods and definitions tend to yield very different results on party size (Hashimoto et al. 2001, Reynolds 2005).

Our study had three purposes. The first was to examine the relationship between fruit abundance and party size of bonobos. This is the first study at Wamba that provides quantitative data on fruit production and party size for a period of more than a year. As mentioned below, bonobos of our study group had not been artificially provisioned for 7 years when we started observation for this study. Therefore, our study provides valuable information on the ecology of bonobos under natural conditions.

The second purpose was to provide data for comparative studies between chimpanzees and bonobos by using the same definition of party size and fruit production. We employed methodologies that had been developed for studies on chimpanzees in the Kalinzu Forest, Uganda (Furuichi et al. 2001, Hashimoto et al. 2001), which would allow for accurate interspecific comparison of the relationship between party size and fruit production.

The third purpose was to reevaluate the results of studies on bonobos at Wamba. Since 1976 when all members of group E, which split into the E1 and E2 groups before 1983, were identified, they were provisioned with artificial food until 1996 when the study was interrupted by civil wars (Furuichi 1989, Kano 1992). Because the bonobos had been given only a small amount of artificial food for a limited time,

researchers working at Wamba assumed that the tendencies observed in E1, such as large and stable party size and gregariousness of females, reflected the nature of wild bonobos in an unbiased way. However, there is reason to challenge that these tendencies may have appeared due to the influence of the artificial provisioning. By comparing current and past tendencies of grouping patterns, we may be able to evaluate the extent to which artificial provisioning influenced past studies at Wamba.

## Methods

### *Study Group*

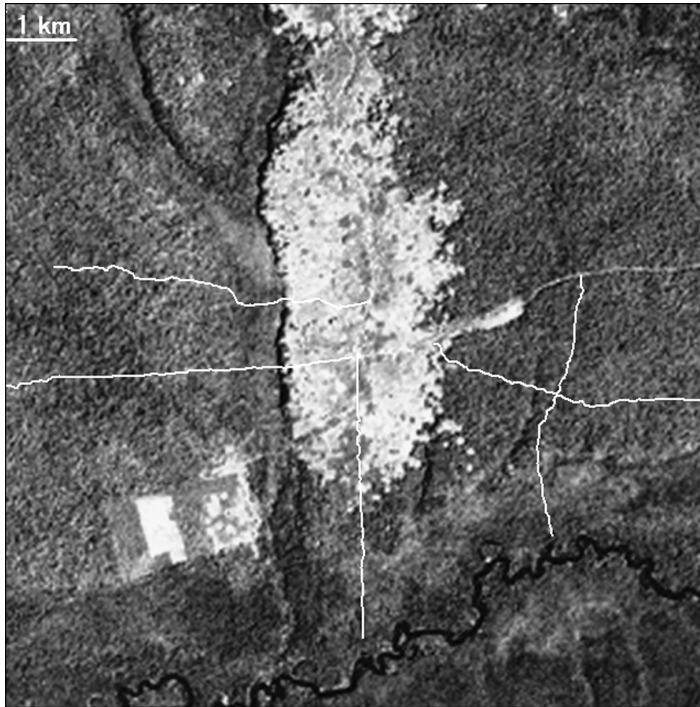
We observed the E1 group (unit-group or community, van Elsacker et al. 1995) of wild bonobos at Wamba in the northern section of the Luo Scientific Reserve, D.R. Congo. The history of E1 and the details of the study site are described by Furuichi (1989), Kano (1992), Hashimoto et al. (1998, 2008), and Idani et al. (2008). In January 2005, E1 included 10 adult males, 6 adult females, 1 adolescent female, 2 juvenile females, 3 infant males, and 1 infant female. Hashimoto et al. (2008) have described the more recent changes in membership of the group.

We observed E1 from September 2003 to December 2005. We attempted to locate parties of E1 and to follow them from sleeping site to sleeping site 6 days per week, for a total of 711 days. During this time, we directly observed bonobos for 484 days, or 68% of the total working days. The total time of direct observation, excluding time spent tracing bonobos by footprints or vocalizations, was 2,216 hours. On average, bonobos were within sight of observers for 4.6 hours per day on days we conducted direct observations.

### *Monitoring Fruit Abundance*

To monitor fruit abundance, we used five line transects and reconnaissance paths, the total length of which is 22,550 m (Fig. 6.1). We used some reconnaissance paths for our survey because they were very narrow trails that ran without avoiding particular types of vegetation and did not seem to affect the growth and fruiting of trees along them. Although the fruit trails were set arbitrarily, they covered various vegetation types in the home range of E1 with minimal bias (Fig. 6.1). We recorded daily rainfall at the research camp, which was situated in the center of the home range.

We walked each trail twice a month. We recorded the number of clusters of fallen fruit that were found within 1 m on each side of the trail, the number of fruits in each cluster, species of fruit, and whether they were ripe or unripe, following the methods used in a study of wild chimpanzees in the Kalinzu Forest, Uganda (Furuichi et al. 2001). As recommended by Furuichi et al. (2001), we evaluated fruit abundance based on the number of clusters of ripe fallen fruits per km of the trail. Although a list of scientific names of 510 plant species found in the study site was available (Idani et al. 1994), a considerable number of unidentified species



**Fig. 6.1** Vegetation in the ranging area of E1 and trails for monitoring fruit abundance. The vegetation image was made from Landsat data recorded on 14 January 1991 (Hashimoto et al. 1999). Pale areas include agricultural fields and young secondary forest. Medium-colored areas include old secondary forest and primary forest. Dark areas around the river represent swamp forest.

were recorded during our study. Therefore, we used identifications based on vernacular names to represent the number of fruit species.

### *Party Size and Composition*

To obtain data comparable to those for chimpanzees, we employed the definition of the 1-hour party size proposed by Hashimoto et al. (2001) for evaluating party sizes of chimpanzees. While following a party, we recorded the number of bonobos within each 1-hour segment. We recorded the names of bonobos in sight at the beginning of each hour and continued recording bonobos that appeared in sight until the end of the hour. Thus, the 1-hour party represents the minimum number of bonobos that were present in the party during each 1-hour observation. We also recorded the number of minutes for which bonobos were in sight of observers in each 1-hour segment. Through this information, we were able to attain reliable data on the 1-hour party size.

For the comparison between chimpanzees and bonobos, we used data for chimpanzees of the M group in the Kalinzu Forest Reserve, Uganda that we collected during

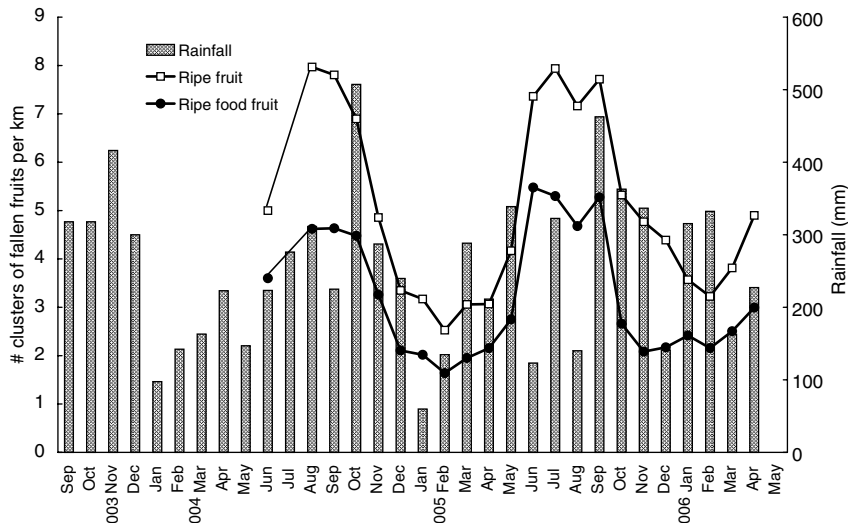
the 1997-1998 study period, using a similar 1-hour party method (Hashimoto et al. 2001). Because members of M had not yet been fully identified at that time, for the calculation of relative party size, we used the group size and composition recorded in 2005: 19 adult males, 22 adult females, 4 adolescent males, 9 adolescent females, 6 juvenile and infant males, 9 juvenile and infant females, and 1 infant of unidentified sex. We assumed that this 2005 group composition was not largely different from that during 1997–1998 because we did not observe any dramatic change in the membership.

## Results

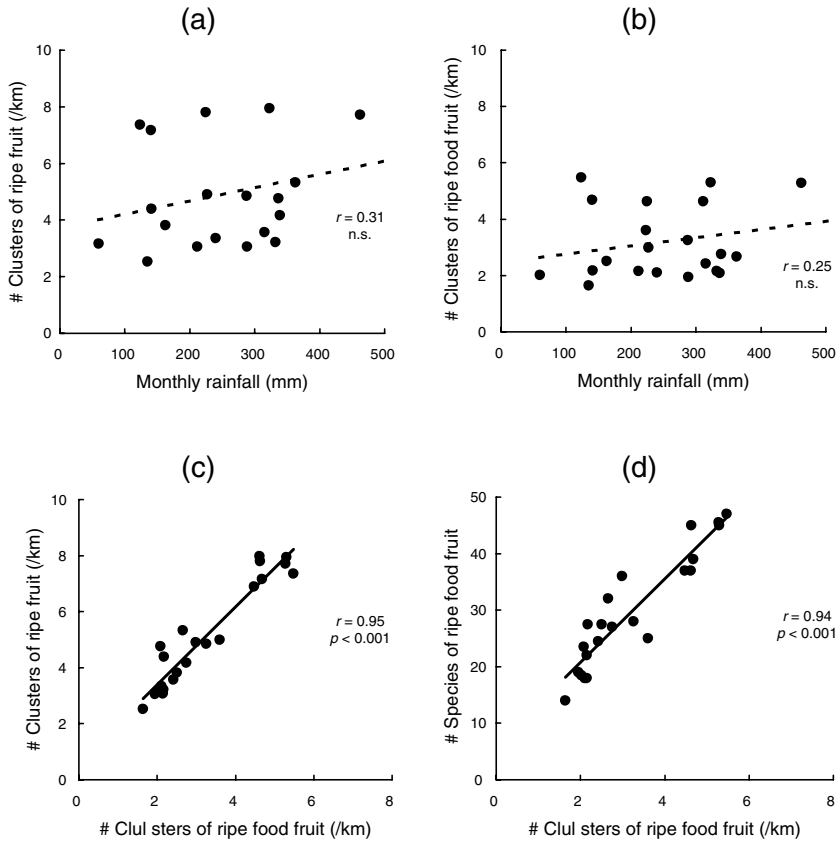
### *Seasonal Changes in Fruit Abundance*

The monthly rainfall and fruit abundance are illustrated in Fig. 6.2. The average annual rainfall was 2,843 mm in 2004 and 2,922 mm in 2005. Although no clear rainy or dry season occurred, more rain in the area occurs around October/November, and less around January/February.

The fruit abundance showed fairly irregular changes. There is no significant correlation between the abundance of ripe fruit and rainfall, or between the abundance of ripe food fruit and rainfall (Figs. 6-3a,b). Food fruits include the species that bonobos ate during the current or past study periods. There is correlation between the abundance of ripe fruit and that of ripe food fruit (Fig. 6-3c). The number of species of ripe food fruits on the trails also showed irregular changes that paralleled



**Fig. 6.2** Monthly rainfall and fruit abundance. The data for fruit abundance were available only for June 2004 and from August 2004 to December 2005.

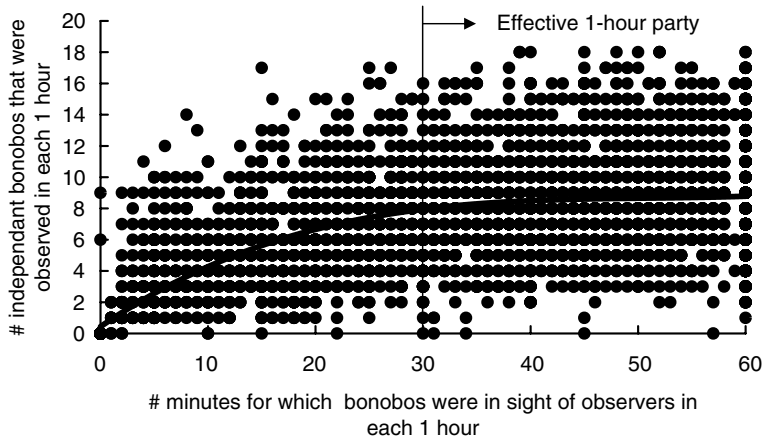


**Fig. 6.3** Correlations between the abundance of ripe fruit and rainfall: (a) the abundance of ripe food fruit and rainfall, (b) the abundance of ripe food fruit and the abundance of ripe fruit, (c) and the number of species of ripe food fruit and the abundance of ripe food fruit (d). Each dot represents 1 month.

the changes in fruit abundance (Fig. 6-3d). These results suggest that rainfall cannot be used as an indicator of fruit abundance as expressed by the number of clusters or species of ripe fruits or ripe food fruits, and that the actual abundance of fruits must be monitored during the same study period to observe the influence of food abundance on ranging patterns or feeding behavior of bonobos.

### *Size and Composition of the 1-hour Party*

Figure 6.4 shows the relationship between the number of bonobos that were observed in each 1-hour segment and the number of minutes for which bonobos were in sight of observers in the same 1-hour segment. The number of bonobos increased



**Fig. 6.4** Relationship between the number of bonobos that we observed in each 1-hour segment and the number of minutes during which bonobos were in sight of observers in the same 1-hour segment. Each dot represents the data for one 1-hour observation.

with the amount of observation time until 30 minutes and then became saturated. Thus, it took about 30 minutes of observation until we confirmed most of the bonobos in a party. We therefore excluded data for 1-hour parties with less than 30 minutes of observation, which may have underestimated the party size. This result also suggests that scanning observations may largely underestimate party size. We termed the 1-hour party size with observation of 30 min or more the effective 1-hour party size. We obtained at least one effective 1-hour party size on each of 465 days; the mean number of effective 1-hour party size per day was 5.1.

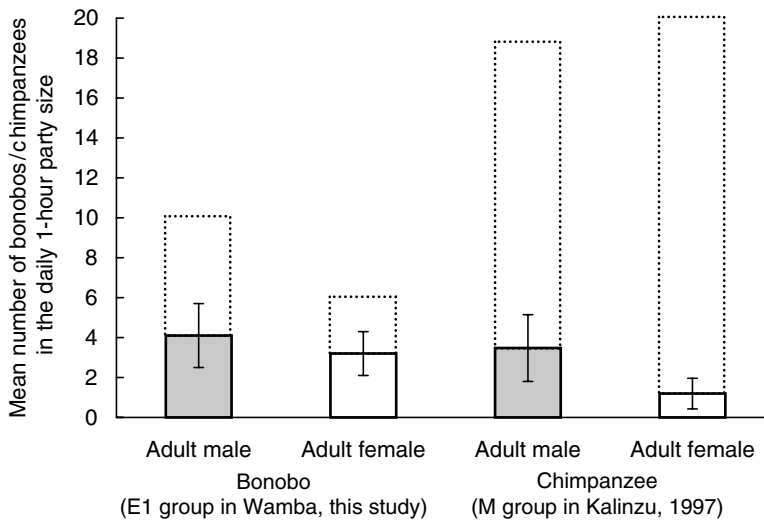
We calculated the 1-hour party size for each observation day, daily 1-hour party size, by averaging the effective 1-hour party sizes for that day (Table 6.1). The mean number of bonobos in daily 1-hour parties was 11.2. The mean number of independent bonobos in daily 1-hour parties was 8.7, which included 4.1 adult males and 3.2 adult females. Thus, as reported in previous studies at Wamba, parties of bonobos in E1 consistently included similar numbers of males and females (Kano 1983, Furuichi 1987).

We also obtained the party size of chimpanzees of the M group in the Kalinzu Forest, Uganda, using the same 1-hour party method. The mean of daily 1-hour party size was 5.9 independent individuals, which included  $3.5 \pm 1.7$  (S.D.) adult males and  $1.2 \pm 0.8$  adult females ( $N = 53$  days).

Figure 6.5 is a comparison of the 1-hour party size between bonobos of E1 and chimpanzees of M. As stated above, the 1-hour party of bonobos includes similar numbers of males and females. However, because E1 contained fewer female members during the observation period, the relative party size, which is the percentage of individuals in the party to the number of all individuals in the unit-group (Boesch

**Table 6.1** Mean number of E1 bonobos in the daily 1-hour party

	Mean	S.D.
Adult male	4.1	1.6
Adult female	3.2	1.1
Adolescent male	0.2	0.4
Adolescent female	0.2	0.3
Juvenile	0.8	0.6
Unidentified	0.2	0.4
<i>Subtotal / Independent individuals</i>	8.7	2.8
Infant	2.4	1.0
<i>Total / All individuals</i>	11.2	3.6

**Fig. 6.5** Comparison of party size and composition between chimpanzees and bonobos. Bars show the mean number of adult males or females in the 1-hour party, and error bars indicate the standard deviation. Bars with dotted lines show the number of members of each sex in the studied unit-groups.

1996), is higher for females. The relative party size was 41% for adult males, 53% for adult females, and 51% for all independent individuals. In chimpanzees, the 1-hour party included a similar number of adult individuals as did the bonobos. However, because the number of unit-group members was much larger for chimpanzees than for bonobos, the relative party size was much lower than in bonobos. In particular, female chimpanzees show a much lower tendency to join parties. The relative party size for M was 20% adult males, 6% adult females, and 13% all independent individuals.

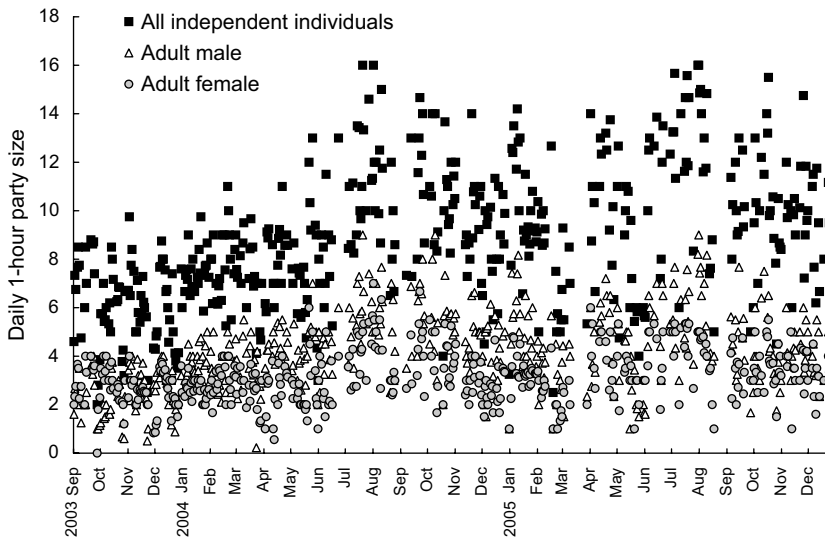


***Relationship of Party Size to Fruit Abundance***

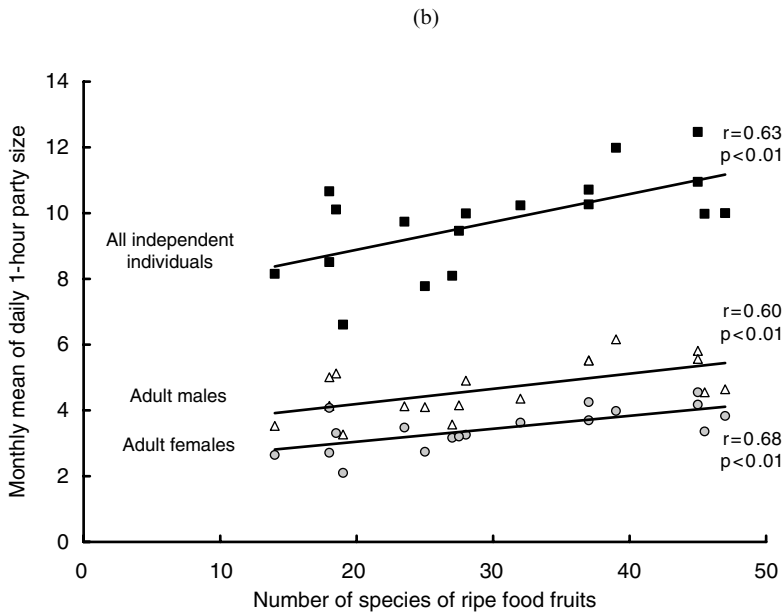
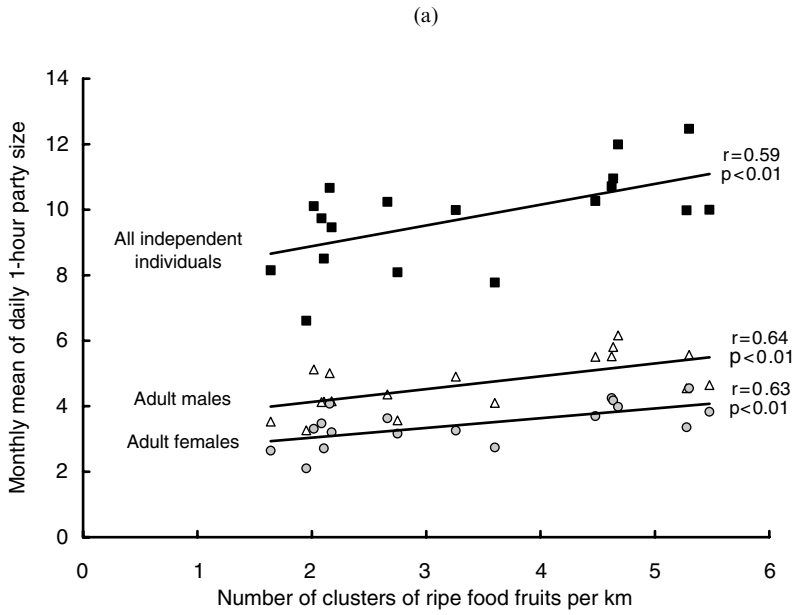
Figure 6.6 shows the daily 1-hour party size of all independent bonobos, adult males, and adult females throughout the study period. Although the sexual composition of the party was quite stable, the party size seemed to show seasonal fluctuations. Therefore, we calculated monthly means of the daily 1-hour party size and compared them with the abundance of ripe food fruits in each month as expressed by the number of clusters of fallen fruit on the trails. As shown in Fig. 6.7a, the number of all independent individuals is significantly correlated with food fruit abundance. The number of adult males and the number of adult females are also significantly correlated with the abundance of food fruit. In addition, we analyzed the correlation of the party size with the number of species of food fruit that were found on the fruit trails each month. The number of all independent individuals, the number of adult males, and the number of adult females are all significantly correlated with the number of species of food fruit (Fig. 6.7b).

**Discussion**

We found that E1 formed a large stable party that included both males and females. The mean 1-hour party size was 11.2 for all individuals and 8.7 for independent individuals. Although the methods of estimating party size differ between studies, E1



**Fig. 6.6** Daily changes in the daily 1-hour party size. Each dot represents data for 1 day.



**Fig. 6.7** Relationship of monthly average of the daily 1-hour party size to (a) the abundance of ripe food fruit in a month and (b) to the number of species of ripe food fruit in a month. Each dot represents data for 1 month.

mean party size is within the range of those for bonobos in previous studies. It is smaller than the 16.9 (Kuroda 1979) and 18.9 (Kano 1982) previously reported for E from which E1 split, and it is larger than the 8.5 mean party size for bonobos at Yalosidi, D.R. Congo (Kano 1983). It is also larger than the 7.9 (Badrian and Badrian 1984), 5.4 (independent individuals, White 1988), 5.4 (independent individuals, Malenkey and Stiles 1991), 6.4 (independent individuals, Chapman et al. 1994), and 4.9 (independent individuals, Hohmann and Fruth 2002) mean party sizes of Lomako bonobos.

The party size of bonobos in our study is larger than that of the chimpanzees of M group in the Kalinzu Forest, and of chimpanzees in most other populations (Chapman et al. 1994, Reynolds 2005). Boesch (1996) suggested that mean party size should be expressed as a percentage of the total community (or unit-group) size, and showed that the relative mean party sizes of chimpanzees over the study periods were between 9 and 21% of the unit-group size. The relative mean party size of chimpanzees of the M group in Kalinzu (13%) falls within this range, and Hohmann and Fruth (2002) reported that the known relative party size for chimpanzees falls between 9 and 30%. However, the relative party size of Lomako bonobos is in the higher part of the range (27%, Hohmann and Fruth 2002), and that of E1 (51%) is far beyond it. Thus, the party size of E1 bonobos seems to be larger than that of chimpanzee populations both in absolute number and in percentage of the unit-group size.

For bonobos of E1, the relative party size was larger for adult females than adult males, indicating that individual females joined mixed parties more frequently than did individual males. This result corresponds with past reports for E1 (Kano 1982, 1992, Furuichi 1987), and reports for Lomako bonobos (White 1988). This is a marked difference from chimpanzees of M group in Kalinzu, in which the relative party size was much smaller for females than for males. The lower gregariousness of females is a common feature among chimpanzees (Wrangham 1979, 2000, Janson and Goldsmith 1995, Williams et al. 2002, Reynolds 2005). Thus, the differences in grouping patterns between chimpanzees and bonobos are not only reflected in the party size, but also in the reversed sociality of males and females. Many researchers have argued about these differences with reference to the high social status of females, prolonged estrus of females, and moderate contest competition for food resources (Furuichi 1989, Wrangham 1986, Kano 1992, Chapman et al. 1994, Furuichi and Hashimoto 2002), suggesting that more studies are needed to resolve the issue.

The relationship between seasonal changes in fruit abundance and party size has also been debated by many researchers. A general consensus exists that party size may increase during periods of fruit abundance (Janson and Goldsmith 1995). Some studies have shown that chimpanzees may form larger parties during seasons with higher fruit abundance (Wrangham 1977, Ghiglieri 1984, Isaberya-Basuta 1988, Boesch 1996, Matsumoto-Oda et al. 1998). However, there are contradictory findings for different populations of chimpanzees. Isaberya-Basuta (1988) reported that the positive relationship between fruit abundance and party size did not hold when multiple sources of important foods were available. Stanford et al. (1994)

reported that the party size of chimpanzees in Gombe, Tanzania was largest in the dry season when the food supply was restricted. Boesch (1996) suggested that marked differences occurred among years in the relationships between fruit abundance and party size. Newton-Fisher et al. (2000) and Hashimoto et al. (2001) reported that in chimpanzees of Budongo and Kalinzu, Uganda, fruit abundance did not have a significant influence on the party size, while the presence or number of estrous females did. Basabose (2004) also reported no positive relationship between fruit abundance and party size in Kahuzi-Biega, D.R. Congo.

Our results on bonobos indicated a significant correlation between food fruit abundance or number of species and party size in terms of the number of adult males, adult females, and independent individuals, though the increase in party size with the increase in fruit abundance was very small. These results are compatible with earlier reports on bonobos. Kuroda (1979) reported that party size of Wamba bonobos became larger when preferred fruits were abundant. For Lomako bonobos, White (1998) showed that the number of independent individuals and adult males in the party significantly increased with fruit abundance, while there was no significant correlation for adult females. Hohmann and Fruth (2002) reported that for Lomako bonobos, the number of independent individuals, adult males, or adult females in the party had no significant correlation with fruit abundance, but the number of adult females significantly correlated with the number of fruit species consumed by bonobos in each month.

Although it may be premature to conclude a general tendency for bonobos based on such a small number of reports, it seems that the variation in the correlation of party size and fruit abundance is smaller for bonobos than for chimpanzees. In chimpanzees, the presence or absence of estrous females dramatically influences the number of adult males that join a party (Matumoto-Oda et al. 1998, Newton-Fisher et al. 2000, Hashimoto et al. 2001). This factor may mask the influence of fruit abundance on party size in some studies. In bonobos, however, some estrous females usually are present because many females exhibit pseudo-estrus even during the infertile periods (Wrangham 1986, Furuichi 1987, Kano 1992, Furuichi and Hashimoto 2002). Furuichi and Hashimoto (2002) reported that in a group of Wamba bonobos, a fairly constant number of estrous females were present throughout the study period ( $3.1 \pm 1.1$  [S.D.], range 1–5,  $N = 57$  days in 1985/1986;  $3.1 \pm 1.9$ , range 1–7,  $N = 48$  days in 1987/1988;  $4.1 \pm 1.5$ , range 2–8,  $N = 43$  days in 1990/1991). Although Hohmann and Fruth (2002) reported that parties in which mating occurred were larger than average, the difference seemed to be very small. The usual presence of estrous females and the moderate fluctuation in their numbers in the unit-group or community of bonobos may cause the correlation between fruit abundance and party size to appear as it does.

We conducted our study on the bonobos of E1 under completely natural conditions. Because artificial provisioning had been terminated 7 years before the study, we assumed that its influence on the ecology or behavior of the bonobos was negligible. The results of this study, including the formation of large mixed parties, higher sociality of females, and positive correlation of party size with seasonal fruit abundance, closely resembled the results of studies that had been conducted while the

bonobos were artificially provisioned. This is probably because bonobos received only a small amount of food during a limited period of time when they were artificially provisioned (Furuichi 1989, Kano 1992).

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