



Seasonality and Socioecology: The Importance of Variation in Fruit Abundance to Bonobo Sociality

Frances J. White¹

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The assumption that nonseasonal, evergreen, rain forests contain more continuously available food resources than seasonal rain forests is fundamental to comparisons made between the socioecology of the male-bonded Pan troglodytes and the female-based social system of the Pan paniscus. Chimpanzee females may be less social due to the high costs of feeding competition, whereas in the more food-rich central African rain forests such as the Lomako forest, female bonobos can associate and socially bond. The Lomako Forest experiences two wet and two dry seasons a year. Data on fruit abundance and sociality show that despite monthly variation in fruit availability, there was no consistent seasonal variation in fruit abundance or dietary breadth. Bonobo use of nonfig fruits, figs, THV, and leaves did not follow seasonal patterns. Leaves and THV may act as complementary sources of plant protein and their use was inversely correlated. Monthly variation in fruit abundance was associated with a significant decrease in the number of males in a party but not in the number of females. Focal males were frequently solitary during 1 of the 3 months with the smallest party sizes. In contrast, females remained social with each other throughout the year. Therefore, seasonality at Lomako appeared to be less marked than at comparable chimpanzee sites, such that the variation in fruit abundance did not fall below a level that prohibits female sociality.

KEY WORDS: *Pan paniscus*; bonobo; seasonality; feeding; social bonds.

¹Biological Anthropology and Anatomy, Duke University, Durham, North Carolina 27708.

INTRODUCTION

The two species of *Pan*, the chimpanzee, *P. troglodytes*, and the bonobo, *P. paniscus*, have different social systems. The social organization of *Pan troglodytes*, as described for study populations of the subspecies *P. t. schweinfurthii* at Gombe and Mahale Mountains, is male-bonded (Goodall, 1986; Nishida, 1979). Males are gregarious, and cooperate with male relatives to defend a communal range that includes the feeding ranges of several unrelated females (Goodall *et al.*, 1979; Nishida, 1979). These social males are highly affiliative toward each other and form frequent and protracted grooming partnerships (Goodall, 1968). In contrast to these social males, female *Pan troglodytes* are rarely affiliative toward each other (Bygott, 1979). Females live their lives in semisolitude with their young in overlapping core areas (Halperin, 1979; Wrangham, 1979a, b). Although there is variation in aspects of the social systems of other populations and subspecies of *Pan troglodytes*, this male-bonded pattern appears to be consistent (Tutin *et al.*, 1983).

In contrast, bonobos exhibit a female-biased social system (White, 1989). Unlike *Pan troglodytes*, *P. paniscus* has a social organization characterized by high affiliation among females and between males and females, but not among males (Kuroda, 1979; Kano, 1982; Kitamura, 1983; Badrian and adrian, 1984; White, 1988, 1989, 1992b; White and Burgman, 1990; Furuichi, 1987).

Earlier examinations of the differences in social organization of chimpanzees and bonobos supported the hypothesis that bonobos have a reduced level of feeding competition that permits larger parties (White and Wrangham, 1988). Feeding competition among bonobos may be reduced by the use of larger food trees or the use of alternate food sources such as high-quality terrestrial herbaceous vegetation (THV), which is either not available or available and not utilized by chimpanzees.

The level of arboreal feeding competition among Lomako's bonobos is lower than that for Gombe chimpanzees (White and Wrangham, 1988), supporting the hypothesis that bigger food trees for bonobos may permit greater female sociality. In contrast, a recent test of these ecological parameters for rain forest chimpanzees at Kibale by Chapman *et al.* (1994) showed that Kibale chimpanzees use patch sizes that are comparable to those at Lomako even though female-female affiliation at Kibale is similar to that of other populations of *Pan troglodytes* (Wrangham *et al.*, 1992). The relationship between patch size and feeding competition differs between the two species: the amount of food removed from large patches at Kibale was not dependent on the number of animals present. However, the Kibale study recorded DBH (diameter at breast height), while the

Lomako study recorded the canopy radius as the measure of tree size, so that these differences may be methodological. Chapman *et al.* (1994) suggested two possible conclusions. First, the two species may deal with the same spatial variation differently such that parties *Pan troglodytes* divide among several fruiting trees so that individuals spread out whereas *Pan paniscus* forage cohesively. Second, we suggest that the two species may experience different amounts of variation in the levels of feeding competition throughout the year. Under this second hypothesis, *Pan troglodytes* would experience greater variation in feeding competition so that, for at least part of the year, the lack of large food patches prohibits female sociality and removes the advantages of year-round female cohesion. In contrast, *Pan paniscus* would experience less variation in feeding competition allowing females to remain social throughout the year.

Support for the importance of variability in food in the socioecological differences comes from examinations of monthly mean party sizes (White, 1996). Party sizes are, on average, smaller for more months in *Pan troglodytes* at Kibale than in *Pan paniscus* at Lomako for communities of equivalent sizes. Bonobo party sizes also vary with monthly food patch size (White, 1996), with the smallest parties in October and November, approximately the period of lowest fruit production at Lomako (Malenky, 1990). A similar relationship between chimpanzee party size and fruit abundance is seen at Kibale (Wrangham *et al.*, 1992). Therefore, party sizes are determined by fruit availability in both species, suggesting that the smaller parties in *Pan troglodytes* are associated with worse fruit shortages than in *Pan paniscus*.

At Kibale, the variation in both party size and fruit abundance show a seasonal pattern (Wrangham *et al.*, 1992). Furthermore, at Tai, *Pan troglodytes* respond to the minor dry season when fruit is apparently scarce with smaller party sizes (Doran, 1997). Therefore, seasonal variations in fruit production are consistent with party size variation in *Pan troglodytes*. This suggests that bonobos may experience less seasonal variation in fruit abundance so that feeding competition remains low throughout the year thus allowing constant female sociality. It is also possible that bonobos use a fallback food or keystone resource (Terborgh, 1986) such as THV (Wrangham *et al.*, 1996) or figs during periods of fruit shortage to reduce feeding competition and allow female sociality despite variations in fruit abundance.

I examine the impact of seasonal variability in food sources, including keystone resources at Lomako on bonobo sociality. I compare data from phenological fruit trails and dietary breadth, including the use of THV and figs, together with gross measures of habitat productivity (rainfall), with measures of sociality in male and female bonobos to see if Lomako bonobos experience less seasonality in food availability than chimpanzees do.

METHODS

Study Site and Study Population

The study area is the Lomako Forest bonobo study site in the Province of Equateur in the Democratic Republic of the Congo. Situated at 0°51'North, 21°5'E, it consists of approximately 40 Km², with a well-established and mapped trail system. The study area covers a mosaic of forest types, but is principally climax evergreen and polyspecific rain forest (75.2 % of study site), with some areas of second-growth, slope, and swamp forest (White 1992a). The subjects use all forest types, but spend the vast proportion of time in the undisturbed climax forest (93.4% of focal sampling; White, 1992a).

The site includes overlapping ranges of two communities: the Hedon (Bakumba) and the Ranger (Eyengo) communities. I identified a separate, small group (the Blobs) centered on 3 presumably immigrating adolescent females and followed them in 1984–1985. By 1991, they were central reproductive adults within the Hedon community. Data presented here are from 428 hr of focal animal observations of feeding and party sizes on ≥ 85 individuals made in September 1983 to April 1984, October 1984 to May 1985, June to August 1991, June to August 1995, and July to August 1996.

Data Collection and Analysis

Rainfall was available for 48 complete months between 1980 and 1987. Data are available for all months (Fig. 1). Months are classed as dry season if the average rainfall is < 150 cm. This definition differs from that of Malenky and Wrangham (1994) in that December becomes a dry season month and August a wet season month.

I measured fruit abundance and the number of fruiting species for a 13-month period (September 1983 to September 1984) using fruit trails. Fruit trails were used rather than fruit traps as they have proved more effective for large areas such as bonobo community ranges (Malenky *et al.*, 1993). I established 3 non-overlapping 6-km fruit trails along research trails. Together the fruit trails spanned all of the study site. The trails sample all forest types, with 67.1% being through primary forest, 7.8% through Bolafa (*Gilbertiodendron*) (Bolafa) forest, 2.9% through swamp forest, and 21.3% through secondary forest. This differs somewhat from the focal animal range which includes 75.2% primary forest, 9.9% Bolaf (*Gilbertiodendron*) forest, 12.6% swamp forest, and 2.3% secondary forest (White, 1992a), in

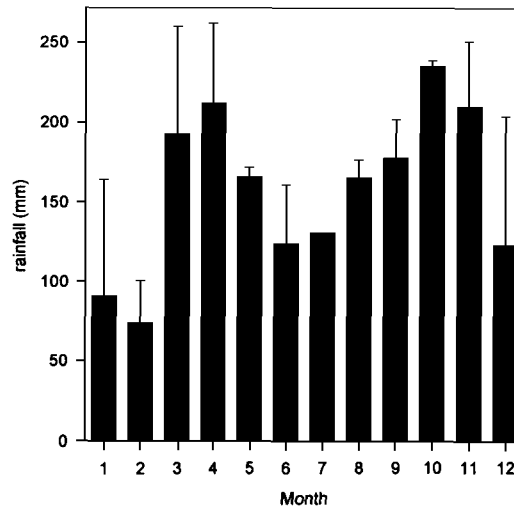


Fig. 1. Precipitation for months in which rainfall was measured daily for 48 complete months between 1908 and 1987 (mean and standard error). Samples sizes vary by month: January $n = 6$, February $n = 6$, March $n = 6$, April $n = 6$, May $n = 4$, June $n = 3$, July $n = 1$, August $n = 2$, September $n = 3$, October $n = 2$, November $n = 4$, and December $n = 5$.

overrepresenting secondary forest and underrepresenting the other forest types.

I sampled each fruit trail in turn for an average of 8.7 fruit trails per month and 113 fruit trails over 13 months. I counted the total number of fruits on the ground in the 0.5-m wide trail and identified them to species. Fruits are food species if there was any record of them being consumed by Lomako bonobos. I combined data from focal sampling during all field seasons on 24 plant species with published observations and fecal samples from Badrian and Malenky (1984) and Malenky (1990) for a total of 64 known food species. All abundances and counts of fruiting species refer to these known fruit food species unless otherwise stated. I summed the total amount of these fruits on the trail on a weekly basis for a total of 45 weeks and divided them by the number of fruit trails walked to give a weekly measure of fruit abundance per fruit trail. I compared these values to the weekly number of food species per fruit trail using non-parametric Kendall rank correlation (Sokal and Rohlf, 1995) to see if the number of fruiting species could be used to estimate fruit abundance. Then I compared fruit abundance and the number of fruiting species per fruit trail between the two wet and two dry seasons and between months using ANOVAs (Sokal and Rohlf, 1995).

I use data on feeding by focal animals during all field seasons to calculate a monthly percentage of feeding on 5 distinct food types: nonfig fruits, figs, pith, other plant parts (predominantly new leaves but including flowers and petioles), and fauna (arthropods and vertebrates). I divided months into the two wet and two dry seasons and compared the percentage of time spent feeding on each food type between seasons. I compared the percentage of time spent feeding among all possible pairs of the different food types via non-parametric Kendall rank correlations (Sokal and Rohlf, 1996) to see, for example, if decrease in feeding on one food type is associated with increase in feeding on another.

I calculated monthly dietary breadth from the number of species eaten by focal subjects during all field seasons. Since the duration of focal sampling varied between months, I calculated the rate of number of species eaten per hour of focal sampling and used the values to compare the dietary breadth between months.

I calculated mean party size and composition as determined by the mean number of independent males and females per party for the 9 months of the 1983–1984 field season that had fruit abundance data. I also calculated a monthly mean fruit abundance from the weekly totals of fruits per trail and compared the values to the monthly mean party size via linear regression (Sokal and Rohlf, 1996). I compared the mean party size and composition for other field seasons between wet and dry seasons.

RESULTS

Seasonality

Using the criteria defined above, the Lomako Forest experiences two dry and two wet seasons each year (Fig. 1), with wide variation in the amount of rainfall between the same months in different years. There is no significant correlation between monthly rainfall and total fruit (food and nonfood species) abundance during the 1983 to 1984 field season (0.109 , $n = 8$, not significant).

There was variation in fruit abundance of known food species, with a period of food shortage evident in July during the shorter dry season (Fig. 2). There is no statistically significant difference in either the fruit abundance per fruit trail ($F = 1.64$, not significant) or the number of fruiting species per fruit trail ($F = 1.44$, not significant) for known food species between the two wet and the two dry seasons. There is a significant difference between months for fruit abundance per fruit trail ($F = 3.25$, $p < 0.004$) but not for fruiting species per fruit trail ($F = 1.90$, not significant).

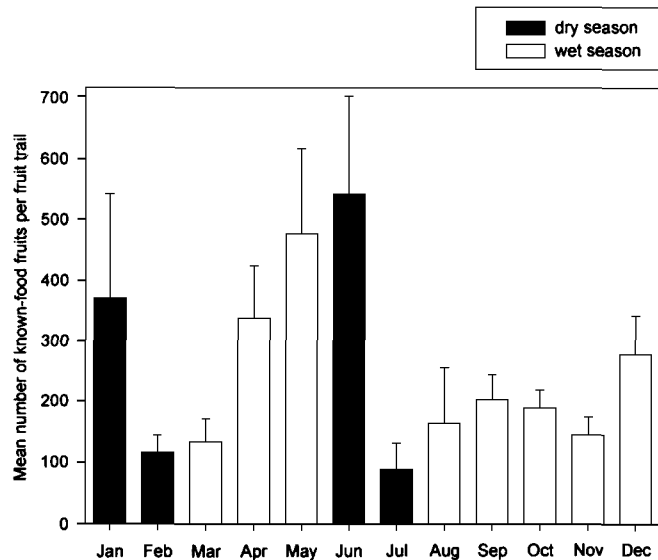


Fig. 2. Mean (and standard error) number of ripe fruits of bonobo food species per trail. Number of fruit trails walked per month: January $n = 8$, February $n = 11$, March $n = 8$, April $n = 6$, May $n = 10$, June $n = 13$, July $n = 9$, August $n = 2$, September (average of 1983 and 1984) $n = 17$ and 5, October $n = 9$, November $n = 10$, and December $n = 7$.

During the 1983 to 1984 field season, there is a significant correlation ($\tau = 0.221$, $p < 0.03$) between the total number of food fruits per fruit trail and the number of fruiting food species per fruit trail.

Fruit Abundance and Party Size

There is a significant regression (Fig. 3) of party size on food abundance as measured by the number of fruits per fruit trail ($F = 5.769$, $p < 0.05$). For party composition there is a significant regression of number of males in parties on fruit abundance ($F = 9.139$, $p < 0.02$) but no significant regression of the number of females on fruit abundance ($F = 0.085$, not significant).

Keystone Foods

There was no clear reliance by the bonobos on a specific food type during specific months (Fig. 4). There is no significant difference in the percentage of time spent feeding on fruits ($F = 0.40$, not significant), figs

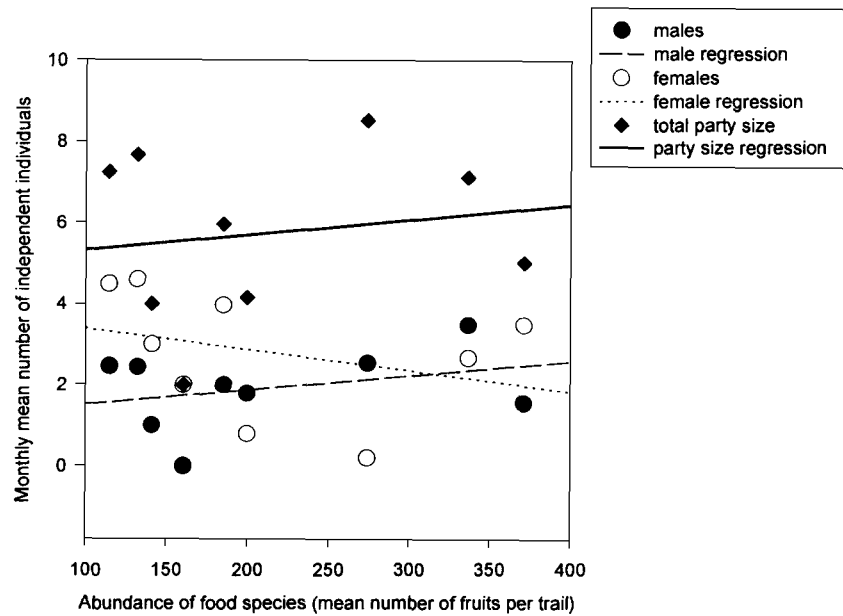


Fig. 3. Regression of mean party size, mean number of males, and mean number of females on monthly mean fruit abundance measured as the number of ripe fruits of known bonobo food species per fruit trail. Party size, number of males, and number of females are averaged from the counts of parties containing the focal animal at each time point (2-min sampling). The mean monthly number of males in parties was zero when all males sampled that month were solitary. Sample size = 9 months from the 1983 to 1984 field season with both party size and fruit abundance data. Regression lines: total party size $Y = 1.151 + 0.027x$, $R^2 = 45.2\%$; males, $Y = -0.519 + 0.009x$, $R^2 = 56.6\%$, and females, $Y = 2.247 + 0.002x$, $R^2 = 1.2\%$.

($F = 0.25$, not significant), pith ($F = 1.72$, not significant), leaves and flowers ($F = 0.58$, not significant), or meat ($F = 0.75$, not significant) among the 4 seasons. The only significant rank correlations between any of these categories are a negative correlation between figs and fruit (Kendall's rank correlation $\tau = -0.719$, $p < 0.002$) and between pith and other plant parts ($\tau = -0.443$, $p < 0.05$). There is no clear indication of bonobos using either figs or THV as fallback or keystone food resources during this time, as the amount of feeding by focal animals on these types of food remained at equivalent levels during all months (Fig. 4). There is no significant correlation between time spent feeding on nonfig fruits and pith ($\tau = 0.123$, not significant) or between all fruits (including figs) and pith ($\tau = 0.198$, not significant). There is also no significant difference in dietary breadth between seasons ($F = 1.85$, not significant). Bonobos fed from a total of 51 nonfig and 13 fig tree species during focal animal sampling. Dietary

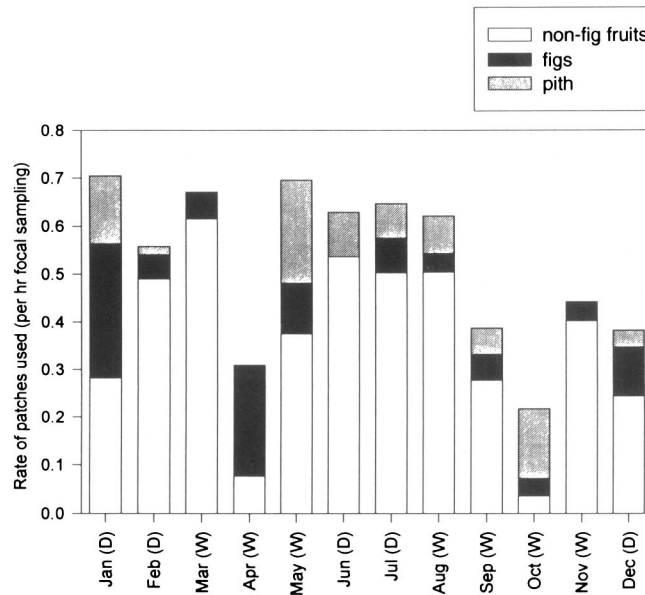


Fig. 4. Number of food patches used per hour of focal sampling. Months are shown as either wet (W) or dry (D) months based on average rainfall. Number of focal hours per month: January, 14.2; February, 59.2; March, 17.9; April, 38.8; May, 18.7; June, 42.9; July, 41.8; August, 25.8; September, 18.1; October, 27.6; November, 24.9; December, 28.8.

breadth is high in the shorter dry season (Table I) and high during the start of the subsequent wet season and in the middle of the longer dry season. It is important to note that I did not estimate the availability of leaves, pith, or meat, so the trends might be related to their availability.

Monthly Variation in Party Size and Composition

The mean party size during focal sampling is 6.73 independent individuals (excluding infants but including unsexed individuals). When parties containing unsexed individuals are excluded, the mean number of independent females is 3.87 and the mean number of independent males is 2.08. On average, the focal animal was solitary for 3.2% of focal sampling. Although the mean party size and number of males and females varied from month to month (Fig. 5), there is no significant seasonal variation in party size ($F = 1.491$, not significant), mean number of males ($F = 1.870$, not significant) or mean number of females ($F = 0.431$, not significant).

Table I. Dietary Breadth Calculated from the Number of Nonfig Trees Species Eaten in Each Month by Focal Animals and Averaged per Hour of Focal Sampling (Does Not Include Herbaceous Foods)

Month ^a	Dietary breadth
Jan. (D)	0.28
Feb. (D)	0.17
Mar. (W)	0.11
Apr. (W)	0.08
May (W)	0.11
June (D)	0.26
July (D)	0.38
Aug. (W)	0.39
Sept. (W)	0.28
Oct. (W)	0.04
Nov. (W)	0.20
Dec. (W)	0.10

^aW, wet; D, dry.

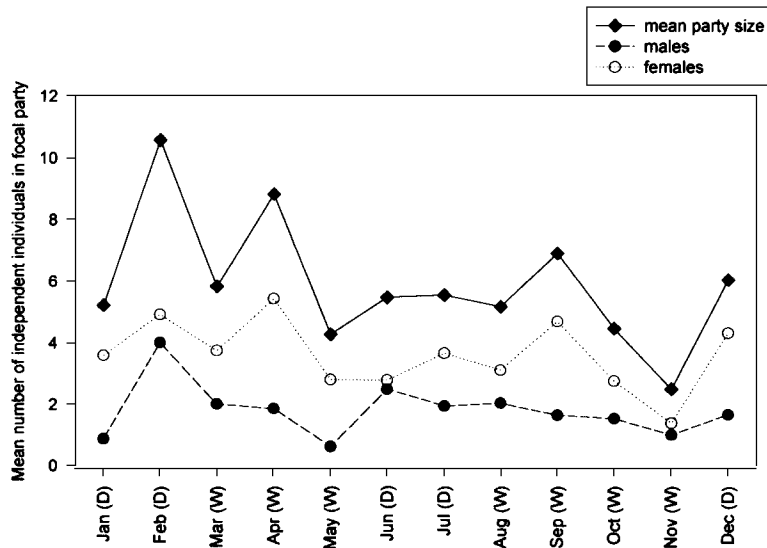


Fig. 5. Mean party size, mean number of males and mean number of females per hour of 2-min focal sampling averaged from 1983, 1984, 1985, 1991, and 1995 field seasons. Months are shown as either wet (W) or dry (D) based on average rainfall. Number of focal hours with complete party counts per month (sample size per month = hrs × 30): January, 14.1; February, 58.3; March, 17.9; April, 38.8; May, 18.7; June, 42.9; July, 41.8; August, 25.8; September, 18.1; October, 27.6; November, 24.9; and December, 28.8.

The mean number of males in focal parties was below 1 for 3 months: 2 wet months (May and November) and 1 dry (January). During November, focal males were alone for 20.7% of focal sampling but were not solitary during the other 2 months. The mean number of females in focal parties fell below 2 for 1 wet month (November), during which focal females were not solitary. Mean focal party sizes were also the lowest for this month.

DISCUSSION

Although the Lomako Forest is less seasonal than other chimpanzee sites in both rainfall and number of tree species fruiting each month (Malenky, 1990), there is evidence of seasonality with less rainfall falling, on average during two dry seasons. There was considerable variation from year to year with some supposedly dry season months having as much rain or more than wet season months in some years, as reflected in the difficulty in defining wet and dry seasons at the study site. As data in this study were pooled over many field seasons, the results presented here should be regarded as trends and interpretation of the results is preliminary.

Fruit abundance showed monthly variation, but not a consistent seasonal variation. Known food species were relatively abundant during the second dry season when their abundance exceeded that during the longer wet season. It is clear from observations that more phenological data across multiple years are needed as some important food species (including some *Dialium* species) produce fruit on a 3- or 4-year cycle. It is also difficult to define food and nonfood species. Dietary breadth increased during periods of clear food shortage and observations showed that foods that would normally be ignored (such as *Gilbertiodendron* seeds) were eaten at these times. Such foods were also usually eaten by peripheral members of communities, especially nulliparous females in the process of immigrating into communities. By including such apparently nonpreferred foods as available food drastically inflates the estimate of food present. While it is difficult to decide which foods should then be considered as preferred foods, it may now be possible to measure the degree to which individuals are nutritionally stressed by measuring urinary ketones to indicate fat metabolism (Knott, 1998).

These data also show no clear evidence that either THV or figs are being used as fallback foods during periods of seasonal food scarcity as both food types were utilized at rates independent of season. However, there is clearly a relationship between the use of figs and other fruits on a monthly basis suggesting that they are in essence providing the same components of the diet and can replace each other. The negative correlation

between use of THV and new leaves suggests that they may function as alternative plant protein sources for bonobos. Although it is generally assumed that THV is consistently available, it may vary in quality between months because the growth rate of the highly preferred large stems is related to the amount of recent rainfall (White, unpublished data). The monthly variation in new leaves and THV quality and quantity may be important factors in the use of these foods and warrants further study.

Anecdotal evidence also suggests a difference in behavior during periods of food scarcity. Visibility of subjects during the short dry season (June to July) at Lomako is typically limited because they spend more time on the ground and in secondary forest or swamp forest. However, parties at Lomako do not become smaller at this time but in fact are as large or larger than wet season parties. There is some indication of differential response by males and females to food shortage in some months but it was males, not females, that were more often alone or in smaller parties.

The impact of temporal variation in food resources on bonobo sociality illustrates the basic difference between the two *Pan* species. The regressions demonstrate that whereas bonobo males responded to lower levels of food availability by becoming less social, females did not. Despite presumably higher levels of food competition during this time, female bonobos were still able to remain in social groups. The smaller size of parties and the lesser number of females per party may have made it possible for one male to monopolize a party of females and exclude others, as has been observed at Lomako (White and Burgman, 1990). The scattered nature of the female parties may also make it more beneficial for individual males to travel between parties in search of other females, thus spending more time alone. These data suggest that despite experiencing some temporal variation in feeding competition, female bonobos may be adjusting their ranging patterns to remain social during times of food shortage. In contrast, although female *Pan troglodytes* can congregate at seasonally available large food trees at Kibale, their basic social pattern is as asocial and uncooperative as observed at other sites (Wrangham *et al.*, 1992).

The hypothesis examined here proposed that the crucial difference between the female-based society of *Pan paniscus* and the male-bonded society of *P. troglodytes* is that bonobos do not undergo a seasonal dietary crunch period when large parties and female sociality are not feasible. The data suggest that, despite some variation in fruit abundance, there was no period when fruit shortage prevented female bonobos from being social. Although the data are limited and any conclusion is preliminary, clearly further study of this important question is needed. The study would require long-term, continual collection of data rather than the field-season based information presented here. These results also emphasize that students of

the behavioral ecology of primates need to examine the temporal variation in foods rather than averaging over a year or over a limited number of months.

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