

Feeding Competition in Lomako Bonobos: Variation in Social Cohesion

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INTRODUCTION

Social organization of chimpanzees (*Pan troglodytes*) has been described by Wrangham (1977; 1979a; 1979b; 1980) in terms of male and female competitive strategies for reproductive success. Females feed in small food patches where high feeding competition prohibits sociality. Males, in contrast, gain greater access to females by cooperating, usually with kin, to defend a large community range containing the core areas of several females.

Although there is variation in aspects of the social systems among populations of chimpanzees, this male-bonded pattern appears consistent (Tutin *et al.*, 1983; Nishida, 1979; Goodall, 1986). The bonobo (*Pan paniscus*), in contrast, shows a female-biased social system (White, 1989a).

In contrast to chimpanzees, feeding competition in bonobos is low. A large proportion of food patches used by bonobos at Lomako are large fruit trees. These large trees represent superabundant food sources where the amount of food removed is dependent only on the number of animals present (White, 1986; White and Wrangham, 1988). Female bonobos can, therefore, afford to be more social, and may further benefit from greater sociality through female defense of food patches from other females (White, 1986) or protection from harassment of females by males (Wrangham, 1986).

Investigations at Lomako Forest (Badrian and Badrian, 1984; Badrian and Malenky, 1984; Thompson-Handler *et al.*, 1984; White, 1986; 1988; 1989a; 1989b; White and Burgman, 1990) and at Wamba (Kuroda, 1979; 1980; 1984; Kano, 1980; 1982; Kano and Mulavwa,

1984; Kitamura, 1983; Furuichi, 1987; 1989) have both spanned several years and provided much of the information currently available on the behavior of the bonobo.

There are some differences in bonobo social organization between study sites (Kuroda, 1979; Kano, 1982; Kitamura, 1983; Badrian and Badrian, 1984; White, 1988; in press). At Wamba, there is frequent affiliation between males and females in many aspects of social organization including interactions (Kano, 1980; Kuroda, 1980; Kuroda, 1984; Furuichi, 1987; 1989) and party composition (Kuroda, 1979; Kano, 1982; Kitamura, 1983; Furuichi, 1987; 1989). There is also affiliation among adult males (Furuichi, 1989). Affiliation between adult males and their mothers has been recently documented (Kano, personal communication in Nishida and Hiraiwa-Hasegawa, 1987; Furuichi, 1989) and may be an important influence on the social status of males (Furuichi, 1989). Studies at Wamba have found cohesion, if not affiliation, among females, but this is generally considered to be secondary in importance to affiliation between the sexes (Kano, 1982; Kitamura, 1983; Furuichi, 1989).

Studies of the Lomako Forest study population have also found a high degree of affiliation between males and females and among females, but not among males (Badrian and Badrian, 1984; White, 1988; 1989b; in press; White and Burgman, 1990). Studies of party membership and proximity have shown affiliation by party membership and proximity among females as being more significant than associations between males and females, but there are variations between communities that parallel differences in observed party size (White and Burgman, 1990). If changes in these measures of affiliation are examined as a continuum across increasing party size, there are two significant conclusions: (1) as party sizes increase there is a change from female-female associations to female-male associations, and (2) males are attracted into large parties where there are more females. Once in large parties, males maintain proximity to females rather than other males (White and Burgman, 1990). This interpretation is supported by the affiliative interactions observed in parties of different sizes (White, in press). Female-female affiliation predominates in small parties (two to six individuals), whereas male-female affiliation becomes relatively more frequent in medium (seven to ten) and larger (11 or more) parties (Fig. 1).

The shift from a female-female to male-female affiliation with increasing party size may reflect the changing costs and benefits to individuals of sociality. Party size in bonobos is dependent on the size of feeding patches (White, 1986; White and Wrangham, 1988). Food is

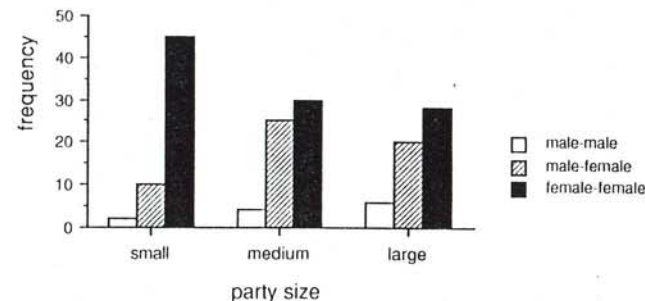


Fig. 1

generally limited in small (less than 10 m radius) food patches, but not in large (greater than 10 m radius) food patches (White and Wrangham, 1988). Feeding competition is, therefore, usually present only in small food patches. Female social strategies may reflect their foraging strategies. As feeding competition decreases, more females join the party. However, these data suggest that there is more association among females at small party sizes where feeding competition is more important. Parties are not, however, passive collections of individuals. There is a high degree of active affiliation among females within parties. Two alternative hypotheses have been proposed to explain the ecological basis of this high degree of female-female affiliation in bonobos. The first hypothesis is that female affiliation represents cooperative alliances among females for the defense of food patches (White, 1986; 1989a). The second is that females group because feeding competition is low and females gain protection from harassment (Wrangham, 1986). The higher female affiliation in small parties may, therefore, represent the greater need for either cooperative defense against other parties of females when food is limited or protection from harassment from males when fewer male protectors are present.

Male social strategies may reflect their ability to gain access to females. Small parties usually contain only one male. When females are in small groups, one male can feasibly monopolize all those present. As party size increases, however, it becomes difficult for one male to exclude others. As party size increases, the proportion of males in parties increases (White, 1988). These males enter large parties in order to maintain proximity with the females (White and Burgman, 1990). Males that are excluded from close association with a small party of cohesive females can join those same females when they associate with other females in larger parties. It may be possible, therefore, for females to manipulate the male membership of a party by changing their association patterns. Males, however, attempt to monopolize specific (usually estrus) females within large parties by excluding other males

from the immediate vicinity of the female. This process, however, is energetically expensive, requires some cooperation from the female, and, if several males are present, is often not successful.

These interpretations are preliminary, and are based on comparisons between communities or on lumped data. At present, the availability of data sets for any one community are not large enough to determine if patterns are consistent within and between communities or to allow a detailed analysis at the level of the individual.

This paper presents further information on changes in social cohesion with the presence or absence of feeding competition. The ranging patterns of female and male bonobos are contrasted with those of the chimpanzee.

METHODS

The Lomako Forest bonobo project study site is located in the zone of Befale, Equateur province in central Zaire (0°51'N and 21°5'E). The study area is predominantly climax evergreen, polyspecific rain forest with small areas of swamp and secondary growth forest (White, 1986). The average annual rainfall is approximately two meters with two peaks, one in October–December and one in March–May. The fauna present at the site is diverse and includes many potential predators (including the leopard, python, and crowned hawk eagle) and food competitors (including seven other primate species, three species of large hornbills and other large frugivorous birds).

The data represent 546 hours from two independent studies of 302 (FJW) and 244 (AL) hours of observation between July 1983 and July 1986. Unless otherwise stated, the data sets are analyzed separately. The study population is divided into three distinct units: two communities, the "Hedons" and the "Rangers"; and a small splinter group, the "Blobs." During two-minute focal animal sampling (Altmann, 1974) of the first (FJW) study, the distance between the focal animal and its nearest neighbor was recorded. The amount of food removed from a patch was estimated in "bonobo-minutes" from the number of animals eating at each timepoint summed for each visit to a feeding tree (White and Wrangham, 1988). Food patches were then divided into those with limited food and feeding competition (less than 10m radius) and those with superabundant food and no feeding competition, following White and Wrangham (1988). The second study (AL) used five-minute scan samples. Interactions were recorded opportunistically during both studies.

The party size was determined at the start of each sighting and after

fission or fusion. A party was defined as a cohesive set of individuals that maintained contact. Fusion events were obvious because of the extensive exchange of vocalizations before, and the burst of interactions during and immediately following, fusion. Fission was more difficult to confirm, since large parties often rested dispersed throughout several trees. A party was considered to have undergone fission if individuals left, could not be located resting nearby (within 200m), and did not return within one hour or when the party coalesced for travel.

RESULTS

The mean party size was similar for both studies (5.4 for FJW and 5.8 for AL, both studies combined 5.6, $n=317$). These parties were distinct units, although individuals were sometimes dispersed through many trees when resting. The distance from the focal animal to its nearest neighbor varied with activity (Fig. 2). Resting parties were more cohesive than feeding parties, but individuals were most separated when traveling. Nearest neighbor distances during feeding were divided between food patches with and without feeding competition. More of the variation in feeding distances was explained by the radius in limited food patches, whereas feeding distances showed little relationship with patch radius in superabundant food sources (Figs. 3a and 3b). Feeding distances changed after interactions (Fig. 4). Individuals fed closer together after affiliative interactions and further apart after aggressive interactions.

Bonobo females show a unique homosexual affiliative interaction of genitogenital (GG) rubbing (Kano, 1980). GG rubbing involves two or more females that embrace and rub the anterior parts of their sexual swellings together. Given the special relationship between frequency of GG rubbing and the amount of food removed from a patch (see below), GG rubbing events were divided according to presence or absence of

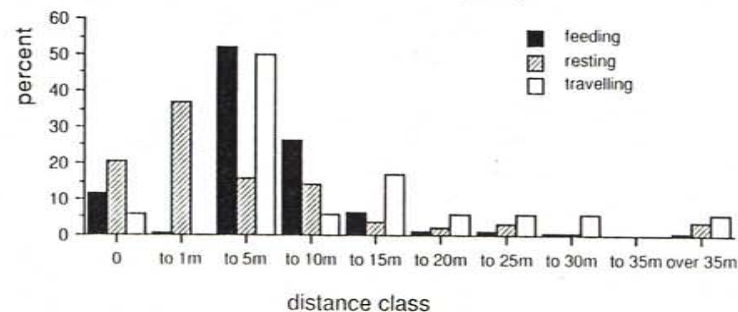


Fig. 2

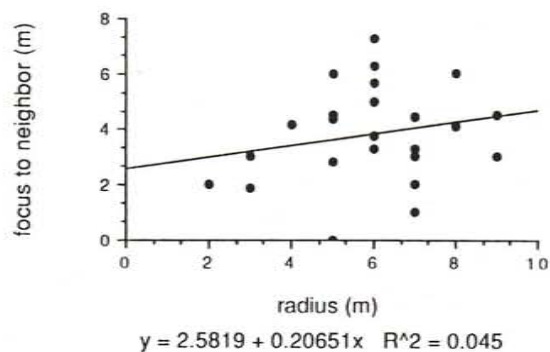


Fig. 3a

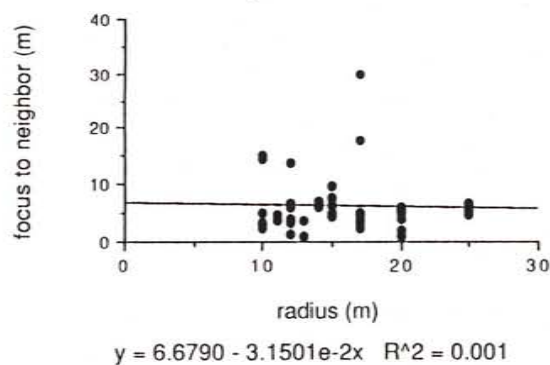


Fig. 3b

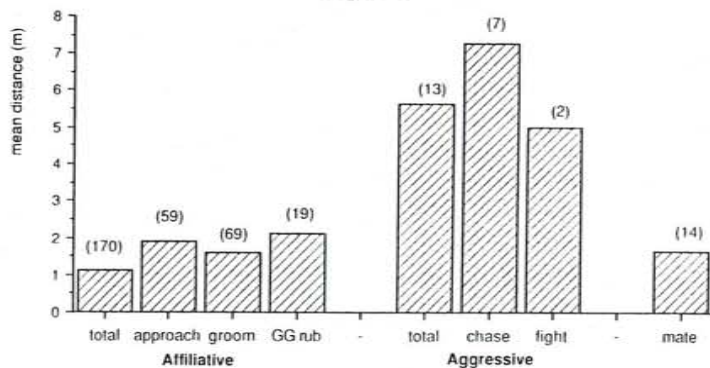


Fig. 4

feeding competition in food patches where first entry into the tree was observed (Fig. 5). GG rubbing did not occur in all food patches. No GG rubbings were observed in the 23 visits to limited food patches. There were no GG rubbings in 24 of the 43 visits to superabundant food

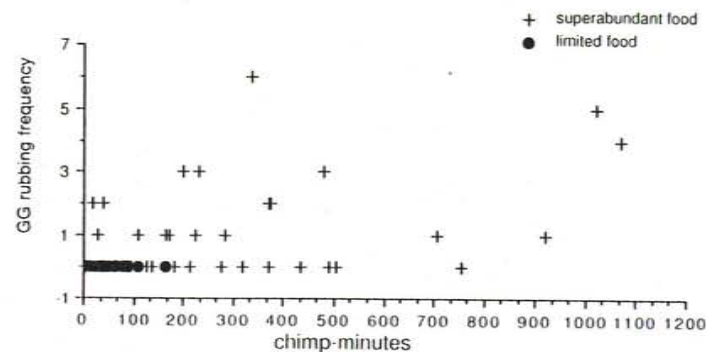


Fig. 5

patches. All GG rubbings occurred in the 19 remaining superabundant food patches.

The minimum ranges of selected individuals were estimated as percentages of the range of the Hedon community over 10 months when continual observations could be made (Table 1). Percentages were used because of difficulties with accurate mapping of the study area. The largest range of 74.7% was covered by an old female with no infant. One of the three females with infants, Tasha, covered a range larger than any male. The average male range, the average female (without infant) range, and the average range of a female with an infant were equivalent.

Table 1. Individual Ranging Areas (Over 10 Months, Minimum Estimate)

Sex class	Range (%)
(individual)	(%)
Female, no infant	
(Miss Flagg)	55.4
(Stubbles)	74.7
(Connie)	44.3
(Ethyl)	32.2
Mean	51.7
Female with infant	
(Tasha/Theo)	70.9
(Mimsie/Matoi)	45.6
(Upsy/Daisy)	32.3
Mean	49.6
Male	
(NoHay)	50.6
(ToeJoe)	58.2
(Smiley)	46.8
Mean	51.9

DISCUSSION

Party sizes at Lomako continue to be small. Individuals within a party, however, may spread out through several feeding trees. When feeding, bonobos do not generally sit closer than one meter, or one arm's reach. Presumably, sitting closer would affect the feeding ability of each individual. Individuals aggregate to rest, but travel dispersed. Dispersed traveling may aid individuals in finding new food sources. When new food trees are located, females often give calls that attract the rest of the party (FJW, personal observation). Small parties in underutilized food patches give food calls that attract others, whereas calls from "full" patches result in avoidance. These observations imply that bonobo parties communicate as to whether spare food is available in a food patch. In order to further examine this hypothesis, it will be necessary to follow several communicating parties at the same time. The decisions made by the individuals in each party on whether to join others will presumably depend not only on information from others on the amount of food elsewhere but also on current levels of feeding competition. Detailed vocal analysis will also be necessary in order to examine for measurable differences in vocalizations that may be conveying such information. This vocal communication on distribution, abundance, and occupation of food patches may also be the mechanism of female defense of food patches. Small parties of females may attract others into larger food patches to form larger, cooperative parties with little cost in increased feeding competition. These larger parties can then prevent displacement of the residents by other large parties. When food is limited, however, the advantages of such cooperation do not outweigh the disadvantages of increased feeding competition, so that when larger parties arrive at limited food patches dominant females usually exclude or displace subordinate females.

Unlike chimpanzees at Kibale (Ghiglieri, 1984), bonobos do not disperse as much as possible when feeding. Regressions on food patch radius or party size explained little of the variation (less than 6%) in feeding distance (White, 1986). There does appear to be an effect of radius on feeding distances when food is limited, although this relationship explains only a small amount of the variation. There is no relationship when food is superabundant.

Affiliative interactions, and mating, result in cohesion during feeding, whereas aggressive interactions result in dispersion. Many matings, and most male-male aggression, occur at the start of feeding bouts. It is not unexpected, therefore, that parties often show cohesion of females with females and males with females. The relatively high

frequency of aggression among males can be related to the male dispersion, such that males often rest far from the rest of the group.

The unique female-female affiliative behavior of GG rubbing has been related to levels of feeding competition (White and Thompson-Handler, 1989, in review). This behavior occurs mostly at the beginning of feeding bouts. The frequency of GG rubbing shows no relationship to party size but is related to the amount of food that will be subsequently removed from the food patch (White and Thompson-Handler, 1989; in review). The frequency of GG rubbing is related to the level of feeding competition. GG rubbing occurs in many superabundant food patches and not in patches with limited food. This affiliation may indicate female tolerance of others under such conditions or may reflect potential alliances among females should patch defense from conspecifics be necessary.

The few data presented here on ranges are not equivalent to data of core areas of chimpanzees (Wrangham and Smuts, 1980). They do, however, support the general impression of researchers at Lomako that female bonobos not in estrus may not have core areas that are smaller than those of males.

Bonobos at Lomako are observed in smaller parties than those at Wamba (16.9, $n=146$, Kuroda, 1982). Although parties at Lomako may be scattered at times, it is relatively easy to identify party members. These small, discrete parties did not aggregate to sleep, often did not meet with other community members for days, and may not associate with particular fellow community members for weeks. At no time have all community members been observed in association. This situation is drastically different from that most recently described at Wamba (Furuichi, 1989) where all unit-group members aggregated almost every night.

Differences in descriptions of the social organization between study sites may reflect the difference in party size between study sites. The combined data of grooming frequency at Lomako does not fit an expected distribution based on the summed frequencies (from Kano, 1980 and Kuroda, 1979) at Wamba (observed frequencies at Wamba: male-male 30, male-female 157, female-female, 88. Observed frequencies at Lomako: male-male 12, male-female 63, female female 55, Goodness of fit test, G (Williams) = 6.027, $p < 0.05$). The two study sites differ in the relative frequencies of male-female to female-female affiliation. If the pattern at Lomako of increasing importance of male-female affiliation with party size is consistent across study sites, this difference may simply be a reflection of the larger parties observed at Wamba.

These important differences between study sites need further investigation. Many factors differ between the two sites, including forest types, predator density, abundance of food competitors, level of habituation, and human influences. A comparison of these possible factors (White, in press) suggests that increased habituation of the Lomako study population is associated with greater differences, rather than more similarity, to that at Wamba. The predation threat also does not parallel differences in party size, as predators are abundant Lomako, where parties are smaller, and absent at Wamba, where parties are larger. Differences in habitat, provisioning, and human habitation may be responsible for differences in party size and composition. It is only through careful comparisons of all the factors that vary between the two sites can we hope to explain this important difference.

SUMMARY

Party sizes of bonobos at Lomako are smaller than those at Wamba. Differences in social organization between the study sites may reflect these differences in party size. When feeding, individuals at Lomako maintain constant distances of about five meters in a wide range of tree sizes unlike chimpanzees which increase nearest neighbor feeding distances in large trees. Individuals aggregate to rest, but travel dispersed. Affiliative interactions decrease and aggressive interactions increase distances between individuals. GG rubbing among females occurs in many superabundant food sources but not in limited food sources. Unlike chimpanzees, bonobo nonestrus-female core areas are not smaller than those of males.

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