Reviewed Article

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Contrasting Chimpanzees and Bonobos: Nearest Neighbor Distances and Choices

Abstract

In an effort to understand factors underlying differences in the social organization of *Pan troglodytes* and *P. paniscus*, we measured the nearest neighbor distances and choices for chimpanzees in Kibale National Park, Uganda, and for bonobos in Lomako Forest, Zaire. We assume that the spatial organization of a set of individuals should reflect the underlying relationships between them. Bonobos were found to have smaller nearest neighbor distances than chimpanzees. The distribution and variability of the distances suggested that chimpanzees have a more restricted range of nearest neighbor distances than bonobos, avoiding situations of very close proximity. Selection of the sex of the nearest neighbor by a focal animal differed between the species. For example, male bonobos rarely had another male as their nearest neighbor, while male chimpanzees frequently did. Similarly, male bonobos tended to move apart when observed together, while it was female chimpanzees who tended to move apart when together. These observations are considered with respect to the nature of the social interactions in these species.

Introduction

There have been a number of attempts to understand the factors underlying differences in the social organization of chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) [1–5]. The social organization of the chimpanzees has been described in terms of male and female competitive strategies for reproductive success, with females competing for

use of small food patches and males attempting to gain greater access to females by co-operating with other males in joint territorial defense [1]. These strategies result in a male-bonded system. In contrast, the social organization of bonobos is viewed in terms of relaxed feeding competition [1, 2, 6] resulting in one that is more female-biased [3] than that of chimpanzees and involves more interactions among females and between females and males [3, 7–10]. However, there has also been increasing documentation of variability in types of social interactions for both species.

In Gombe National Park (Tanzania), female chimpanzees spend little time together and female-female relationships are either neutral or slightly aggressive [11]. In contrast, males are typically found in the company of other males and affiliative male-male interactions are frequent. The nature of the social interactions among chimpanzees at Mahale Mountains National Park (Tanzania) [12], in the Kanyawara community in Kibale National Park (Uganda) [13] and in the Budongo Forest (Uganda) [14] appears to be similar to that in Gombe. In contrast to these studies, the female chimpanzees of Bossou (Guinea) frequently travel, feed and groom together [13, 15 attribute this to the unique ecological setting of Bossou]. At Tai (Ivory Coast), female chimpanzees range over the entire community's range (regardless of their estrous cycle), the majority of females have at least one stable adult female associate with which they share food and form coalitions to support one another [16], but the females tend to forage away from the main core group [17]. Ghiglieri [18, 19] found that female chimpanzees at the Ngogo study site of Kibale National Park associated and groomed with each other more than females did with males (but see Wrangham et al. [13]).

With respect to bonobos, at Wamba and Lomako (Zaire) there is affiliation between males and females in terms of interactions and party compositions (Wamba [7, 8, 20–24]; Lomako [3, 6, 9, 25]; however, the relative importance of affiliation between males and females compared to affiliations among females appears to differ.

In this paper, we present quantitative data on choices of nearest neighbors and distances between nearest neighbors. We collected nearest neighbor distance data, using identical methods, for the chimpanzees at Kibale National Park, Uganda, and for the bonobos of Lomako Forest, Zaire. Patterns of social organization have typically been described by presenting information on social interactions. However, observations of interactions can only be made opportunistically, and many important interactions are relatively infrequent events. In contrast, individuals constantly make decisions concerning the identity of their nearest neighbor and the intervening distance. Thus, the spatial organization of a set of individuals should reflect the underlying relationships between those individuals. This assumes that closeness to a neighbor is an indicator of positive affiliation. This assumption seems reasonable since proximity should reflect the opportunity for positive interactions, like grooming, and the willingness to tolerate some negative effects of proximity, such as increased feeding competition. Further, the choices of which individual to be next to, how far away to be, when to move and how far to move will differ between different activities. The identity of and distance from the nearest neighbor during different activities can help define the strategies of individuals. For example, when the party is resting away from a food source, there is presumably an almost unlimited number of resting sites. The optimal distance to rest away from another individual under such circumstances is presumably not determined by a conflict of interest between the two individuals. In general,

being close to another individual does not affect an individual's ability to rest. But this is not true during feeding. An individual collects and consumes food from its immediate surroundings in a food patch. If one neighbor is sufficiently close to overlap with the feeding space of another, there is the potential for competition between the two for food in the zone of overlap. Thus, feeding too close together can be disadvantageous.

Methods

The Kibale National Park, located in western Uganda (0°13'–0°41' N and 30°19'–30°32' E) near the base of the Ruwenzori Mountains, is a moist, evergreen forest, transitional between lowland rain forest and montane forest [26–28]. About 60% of the Kibale National Park is characterized by tall forest with the canopy generally 25–30 m high, although some trees may exceed 55 m [29, 30]. The remainder of the park is a mosaic of swamp, grassland, plantations of pine, thicket and colonizing forest [28, 30]. The study site, known locally as Kanyawara, is situated at an elevation of 1,500 m [30]. Mean annual rainfall has averaged 1,740 mm (1987–1991) at Kanyawara. The rainfall tends to be well dispersed throughout the year, falling on an average of 166 days per year, but there are two wet and two dry seasons. In 1990, the study community contained at least 41 individuals: 8 adult males, 5 subadult males, 14 adult females, 2 subadult females, 1 juvenile and 11 dependent offspring. 'New' females continue to be observed in the community, thus the number of females is uncertain. Some of these new females may represent new immigrants to the study community, while others may be females that habituated to observers, thus permitting individual recognition and routine observation.

The Lomako Forest Pygmy Chimpanzee Project study site is located in the Equateur Province of central Zaire (0°51' N and 21°5' E) at an altitude of 300 m. The study area is predominantly climax evergreen rain forest, with small areas of swamp and secondary-growth forest [9, 31]. The average annual rainfall is approximately 2,000 mm with two peaks (October–December and March–May). Observations were made on individuals from two separate communities and a splinter group [31].

Tree size, as indicated by diameter at breast height (DBH), in which the chimpanzees of Kibale fed in averaged 100.0 cm DBH (SD = 49.8, n = 49, range = 15–200), while Lomako bonobos fed in trees that averaged 94.2 cm DBH (SD = 50.2, n = 72, range = 15–178). On the basis of field work conducted at Lomako, Malenky [31] reported that the average size of the trees used by bonobos was 88.2 cm DBH (n = 35, SD = 49.7). At Lomako, there are 212 individual bonobo food trees/ha [31], while at Kibale there are 252 chimpanzee food trees/ha [32, 33]. Further, at Lomako, the total basal area of tree species that bonobos used as food sources was 14.2 m²/ha [31], while at Kibale this parameter was 14.0 m²/ha [33]. On the basis of these parameters it would appear that the two areas are ecologically relatively similar.

Observations at Kibale were made between March and December 1990 and May and October 1991, while observations at Lomako were made from July 1983 to April 1984 and from October 1984 to April 1985. At both study sites, the distance between the focal animal and its nearest neighbor and the activity of the focal animal and of its nearest neighbor were recorded at 2-min intervals. When possible, the age, sex and individual identity of the nearest neighbor were noted. When an infant was the nearest neighbor, the distance to the nearest independent individual was used in all analyses. At Lomako, the focal animal was selected from among those individuals in good view so as to attempt to balance observations for each age and sex class. At Kibale, the subject chosen for observation was selected according to a fixed rotation between individual and/or age/sex class in the party. A total of 302 and 229 h of focal-animal observations were made at Lomako and Kibale, respectively. Detailed information on the level of habituation, the duration of sampling, party size and community structure can be found in previously published work on these communities [5, 6, 9, 10, 13, 32, 33].

Statistical analysis of nearest neighbor data is difficult. The distance to a neighbor at one point in time is dependent on the distance at the previous time point. Standard parametric or nonparametric tests assume independence and therefore cannot be used [34]. In this paper we present comparisons of means and variances without a statistical test. Subsequently, we examine this time-dependent series using a method that is based on some association between the position at one time point and the position at the next time point. This involves calculating a transition matrix that contains the probabilities of the nearest neighbor moving from one distance class at one time point to another class at the next time point [6]. The time points are 2 min apart in our samples. The frequencies of starting and finishing in each distance class for each pair of sex of

Fig. 1. The distribution of nearest neighbor distances for chimpanzees studied at Kibale National Park and bonobos studied at Lomako Forest, excluding distances greater than 15 m.
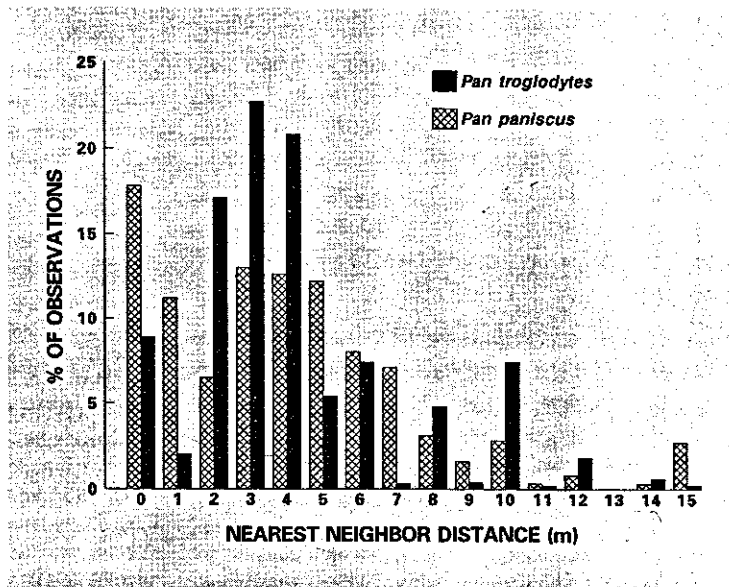
focal animal and sex of nearest neighbor were extracted from the complete data sets for each species. The distance classes were condensed into those closer than 5 m and those farther than 5 m.

Results

The mean nearest neighbor distance for Kibale chimpanzees was 4.1 m (range 0–16 m, n = 968), while for Lomako bonobos the distance averaged 5.5 m (range 0–50 m, n = 2,560). However, at Kibale, it is difficult to see animals that are more than 15 m apart because of visibility limitations associated with the dense vegetation. To make the two data sets comparable, we calculated the mean nearest neighbor distances at Lomako excluding distances greater than 15 m. Such large nearest neighbor distances no doubt occur in Kibale, but they would not have been recorded. The mean nearest neighbor distance at Lomako excluding distances greater than

15 m was 4.0 m (range 0–15 m, n = 2,351). For distances of 0–15 m, the distribution of nearest neighbor distance differs between the sites (fig. 1). At Lomako, bonobos are more evenly distributed throughout all possible distances, while at Kibale the nearest neighbor distances are more restricted. Chimpanzees are less likely to be found at very short nearest neighbor distances. The chimpanzees show a much more peaked distribution, centering around 2–4 m. Similarly, variability in the distance to a neighbor was much greater in bonobos (SD = 7.10 all; SD excluding >15 m = 3.4) than in chimpanzees (SD = 2.1).

The distance to the nearest neighbor varied for both species depending on the activity of the focal animal. For bonobos, the mean nearest neighbor distance while feeding was 5.8 m (SD = 4.8, n = 1,441) for all data and 5.1 m excluding distances greater than 15 m (SD = 2.9, n = 1,366). This represents an increase in distance above the overall mean of 0.3 m for all data, and 2.1 m when excluding distances

Table 1. Sex of the focal animal and sex of the nearest neighbor expressed as a proportion of occurrences (%) for Kibale chimpanzees and Lomako bonobos

	Male-male	Male-female	Female-female	Female-male
All activities				
Pan troglodytes	26.0	12.2	50.6	11.2
Pan paniscus	4.4	19.9	48.3	27.4
Feeding				
Pan troglodytes	13.4	12.9	59.1	14.6
Pan paniscus	5.7	21.5	50.1	22.7

The sex of the focal animal is given first (e.g. male-female represents the proportion of all nearest neighbors recorded for which a male was focal and a female was the nearest neighbor).

greater than 15 m. Similarly, at Kibale nearest neighbor distance while feeding increased by 0.4 m to an average of 4.6 m (SD = 2.6, n = 541).

The mean nearest neighbor distance in all other activities for bonobos was 5.1 m (SD = 9.2, n = 1,119) for all data and 2.5 m (SD = 3.4, n = 985) excluding distances greater than 15 m. In contrast, the nearest neighbor distance for chimpanzees averaged 3.6 m (SD = 3.2, n = 427). The proportions of the total sample represented by feeding bouts and other activities were similar for the two species (bonobos feeding: = 56.3%, other activities = 43.7%; chimpanzees feeding: = 55.9%, other activities = 44.1%). For both species, nearest neighbor distances for resting and travelling were more variable than for feeding distances (coefficient of variation for feeding: bonobos = 82.4%, chimpanzees = 57.6%; for other activities: bonobos = 180.1%, chimpanzees = 88.7%).

For both species, there were age and sex differences in both the average nearest neighbor distance and in the choice of the nearest neighbor. Male chimpanzees had the smallest mean nearest neighbor distance (all activities

mean = 3.1 m, SD = 2.3, n = 290; feeding mean = 3.3 m, SD = 1.3, n = 143); subadult males had a slightly larger mean nearest neighbor distance (all activities mean = 3.8 m, SD = 2.9, n = 159; feeding mean = 1.0 m, SD = 2.0, n = 76), and females had the largest mean distance (all activities mean = 4.7 m, SD = 3.1, n = 464; feeding mean = 5.3 m, SD = 3.0, n = 291). In contrast, bonobo females exhibited a smaller mean nearest neighbor distance (all activities mean = 3.7 m, SD = 3.2, n = 1,792; feeding mean = 4.8 m, SD = 2.9, n = 1,013) than males (all activities mean = 4.8 m, SD = 3.9, n = 514; feeding mean = 5.8 m, SD = 3.1, n = 325).

It is possible to examine the strategies of social interactions used by any age or sex class, by comparing the nearest neighbor distances of a focal animal with those of individuals of specific ages or sexes. Considering all types of activities, when the focal animal was a male chimpanzee, the nearest neighbor was frequently another male (26.0%). In contrast, bonobo males rarely had other males as nearest neighbors (4.4%; table 1). The distribution of nearest neighbor distances when two males were nearest neighbors differed between the
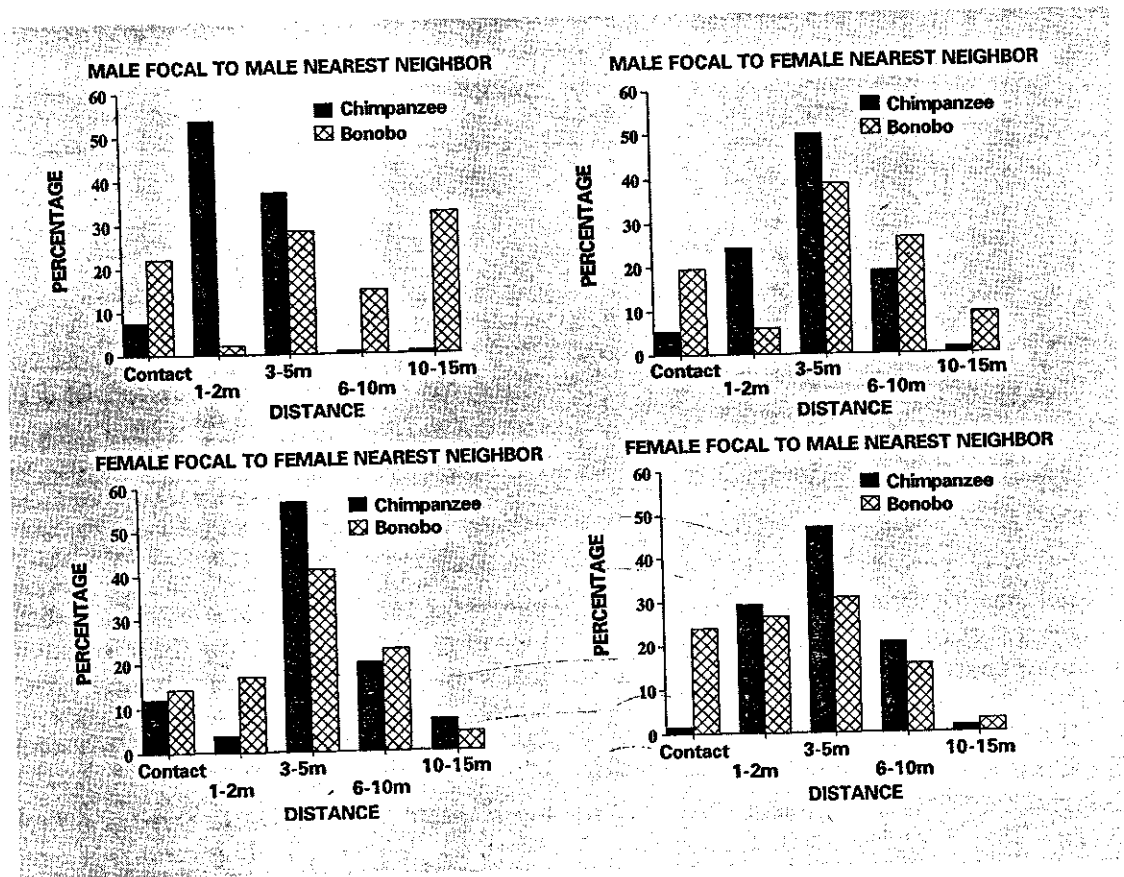
Fig. 2. The distribution of nearest neighbor distances (all activities) for different sexes of focal animal relative to the sex of the neighbor for Kibale chimpanzees and Lomako bonobos (G test, Williams correction; male-male G = 539.9, p < 0.05; male-female G = 45.0, p < 0.05; female-male G = 31.5, p < 0.05; female-female G = 68.8, p < 0.05).

two species (fig. 2). Male chimpanzees frequently had other males within 1–5 m. In contrast, bonobos had a bimodal distribution of male-male nearest neighbor distances; either they were in contact (primarily grooming) or they were relatively far apart (fig. 2). For chimpanzees, the frequencies with which a male and a female were nearest neighbors (male-female; female-male) were lower than the corresponding frequencies for bonobos (table 1). The distributions of these distances were similar, with the exception that male and

females bonobos were more in contact than male and female chimpanzees (fig. 2). The distributions and frequencies for the nearest neighbor of a female being another female were similar for the two species (50.6% chimpanzee, 48.3% bonobo).

While feeding, male bonobos tended to be further away from both other males and other females, while male chimpanzees often fed in close proximity (fig. 3). In contrast, female bonobos tended to feed more frequently at a distance of 1–2 m from another female than
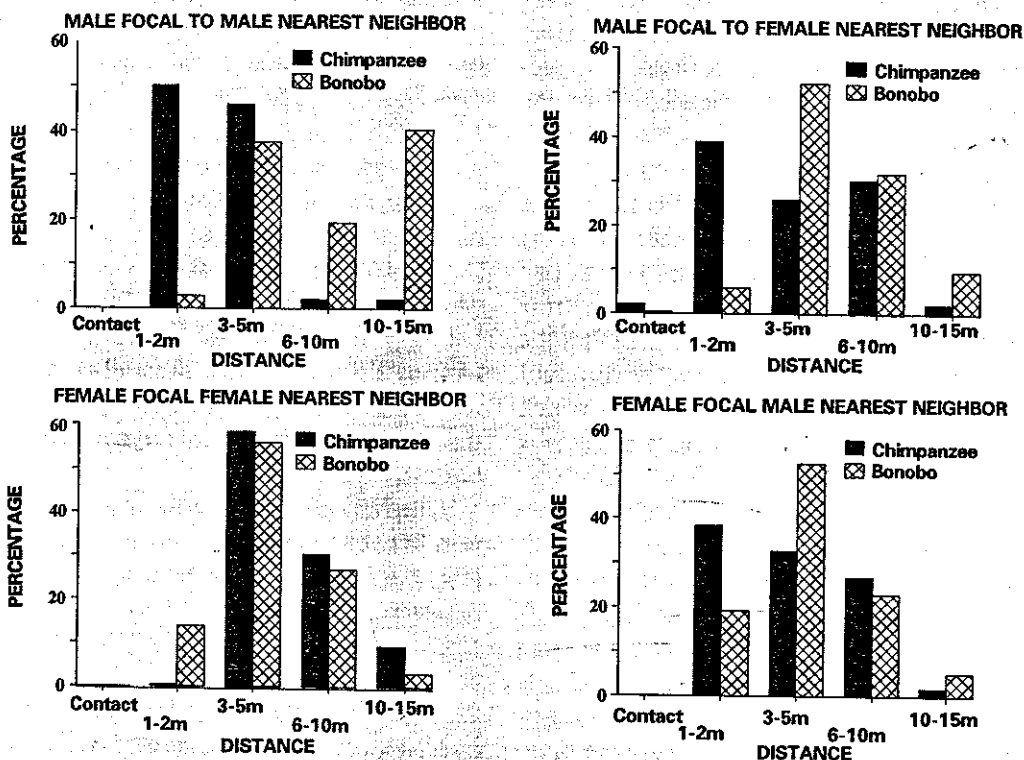
Fig. 3. The distribution of nearest neighbor distances while feeding for different sexes of focal animal relative to the sex of the neighbor for Kibale chimpanzees and Lomako bonobos (G test, Williams correction; male-male G = 134.8, $p < 0.05$; male-female G = 49.7, $p < 0.05$; female-male G = 13.9, $p < 0.05$; female-female G = 74.0, $p < 0.05$).

did female chimpanzees (fig. 3). The frequencies with which either sex had males or females as nearest neighbors while feeding were similar to those found for all activities combined (fig. 2), with the exception that male chimpanzees tended to be close to other males less frequently when feeding than during other activities.

It seems probable that nearest neighbor choice is dependent on factors such as party size, habituation, tree size or habitat-wide food abundance. Some of these factors change slowly. For example, since there is interannual variation in fruit availability, it will take a number of years before a representative range of habitat-wide levels of food abundance is exhibited. Thus, the values presented here should be considered only as preliminary estimates; as more data are collected under a greater variety of circumstances, the data will become more representative of a true species value.

The results presented up to this point indicate that sex may affect the decisions of near-

est neighbor distance and choice. However, statistical comparisons of these data are difficult. The distance to a neighbor at one time point is dependent on the distance at the previous time point. Also, the chances of moving from one distance class to another will depend on the distances represented by each class. Calculating a transition matrix that contains the probabilities of the nearest neighbor moving from one distance class (less than 5 m) at one time point to another class at the next time point (greater than 5 m) demonstrated that the observed matrices are significantly different from an expected transition matrix in which transitions occur at random (chimpanzees $\chi^2 = 877.3$, $p < 0.001$; bonobos $\chi^2 = 983.4$, $p < 0.001$). Therefore, in both species the process is dependent on previous positions.

When the transition probabilities are higher than expected, they are termed 'directive'. Transition probabilities that are lower than expected are termed 'inhibitive'. The direction of the differences of the observed transition matrix from the expected can therefore be examined (table 2). For both species, most cells that involve no movement are highly directive, whereas those involving movement are inhibitive. For bonobos, the only exception to this general pattern is the transition probability of a male focal animal staying within 5 m of a male nearest neighbor. This transition probability is inhibitive. For bonobos, individuals that start close to a nearest neighbor will tend to stay close, unless both the focal animal and the nearest neighbor are male, in which case the two tend to move apart. Chimpanzee males that start off close together tend to stay close together. However, if female chimpanzees start off close together, they tend to move apart. In addition, when male and female chimpanzees start off far apart, they tend to move closer together.

Ghiglieri [18] recorded feeding distances of chimpanzees at Ngogo, another study site in the Kibale Forest (as in this study the maximum nearest neighbor distance was 15 m). He reported a mean feeding distance of 9.5 m (twice that recorded at Kanyawara). The difference between the nearest neighbor distance reported by Ghiglieri and our results for the Kanyawara community in Kibale may relate to party size. Ghiglieri reported a party size half that recently reported by Chapman et al. [33] and Wrangham et al. [13] for the Kanyawara study population. In addition, Ghiglieri typically found parties by waiting at large fruiting fig trees. Thus, if small parties were feeding in large trees, one might expect animals to be spread out with large nearest neighbor distances.

Ghiglieri also reported a negative correlation between party size and feeding distance ($r = -0.67$, $p < 0.05$) and a positive correlation between feeding distances and tree size (indexed as crown volume; $r = 0.82$, $p < 0.01$). For chimpanzees, we found no relationship between feeding distance and tree size (indicated by DBH, $r = 0.014$, $p = 0.864$). To examine the generality of the relationships found by Ghiglieri between party size and nearest neighbor distance, we calculated the correlation coefficient between the mean party size in each food patch and the mean nearest neighbor feeding distance for that patch. For both chimpanzees and bonobos, we found no relationship between these variables (bonobos $r = -0.17$, $p > 0.10$; chimpanzees $r = -0.40$, $p > 0.10$). However, it may not be appropriate to test the relationship between party size and nearest neighbor distance by using the means of both variables for a given patch. For a given food tree, the observer may record a number of different party types: animals that first arrive, one or two animlas that remain behind after the main party has left, etc. Therefore, we also related all party sizes to their respective nearest neighbor distances [bonobos $r = 0.22$, $p < 0.001$, $n = 1,428$, $y = 8.013 + (-0.281x)$; chimpanzees $r =$

Table 2. Directive (+) and inhibitive (−) transition matrices for chimpanzees studied at Kibale National Park, Uganda, and bonobos studied at Lomako Forest, Zaire

Finish		Start			
		<5 m		>5 m	
		male	female	male	female
Pan troglodytes at Kibale National Park					
<5 m	male	+	+	−	−
	female	+	−	+	−
>5 m	male	−	−	+	+
	female	−	−	+	+
Pan paniscus at Lomako Forest					
<5 m	male	−	+	−	−
	female	+	+	−	−
>5 m	male	−	−	+	+
	female	−	−	+	+

0.15, p < 0.0001, y = 7.37 + (−0.152x)]. These regressions explain very little of the variation in nearest neighbor distance. However, the slopes indicate that, as party size increases, chimpanzees decrease their nearest neighbor distances more slowly than bonobos. This suggests that chimpanzees are less tolerant of having other individuals very close to them than bonobos. This observation, in conjunction with the overall distribution of nearest neighbor distances, suggests that chimpanzees avoid situations where the nearest neighbor distance is less than 2–4 m, while for bonobos this is not the case.

Discussion

Nearest neighbor data proved to be useful as indicators of differences in social organization between the two species. Bonobos showed neighbor distances that were smaller on average than those of chimpanzees. Chimpanzees appeared to be less flexible than bonobos in this respect. It appears that nearest neighbor distances are influenced by feeding competition in both species as distances were greater and less variable when feeding than during other activities. During feeding, individuals in close proximity are more likely to compete for the same food item. Such restrictions are less likely to occur during resting or travelling, when close proximity may offer benefits such as social partners or predator/harassment protection [16]. Feeding distances were 0.6 m greater for feeding bonobos than for feeding chimpanzees, which might suggest that feeding competition is lower in bonobos than in chimpanzees. During other activities, bonobo nearest neighbor distances were 1.1 m less than in chimpanzees.

Sex differences in nearest neighbor distances between chimpanzees and bonobos support findings from previous comparisons between the two species [1, 3, 4, 9]. Male chimpanzees were more cohesive and tended to stay in close proximity, whereas females tended to move away from each other. Female bonobos had the smallest nearest neighbor distances and tended to stay in close proximity, whereas male bonobos moved away from other males.

Accumulating evidence suggests that the nature of social interactions in these species is variable. However, the factors responsible for this variability remain unclear. Ihobe's [35] study, which identified differences in male-male relationship between two neighboring communities of bonobos at Wamba, illustrates that the past demographic history of the communities may have a large influence on how social interactions are expressed. Previous attempts to explain the differences in the social organizations of bonobos and chimpanzees have suggested that bonobos have a reduced level of feeding competition. This has been attributed to bonobos either having access to abundant terrestrial herbaceous vegetation [1, 25, 36] or having access to larger [2, 6, 25, 37, 38] or more consistently available [31] food patches.

Chapman et al. [5] propose that the differences in social organization and behavior between bonobos and chimpanzees may have little to do with differences in average party size. They hypothesize instead that the chimpanzee social organization reflects adaptations to extended periods where individuals are forced to be in small parties. In contrast, bonobos are rarely forced to be in small parties. If female chimpanzees were together relatively rarely in comparison to female bonobos, any associations that they would form would be relatively less beneficial, particularly interactions involving cooperative alliances against males. Shifting the emphasis for analyses of mean party size to the proportion of time spent in small parties underlies the importance of studies of the temporal abundance of food resources.

Acknowledgments

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