SOCIAL ORGANIZATION
OF PYGMY CHIMPANZEE

Frances J. White

INTRODUCTION
The family of primates that are most closely related to humans are the Pongidae, or
great apes. There are four species of great apes living today: the orangutan, the
gorilla, and two species of chimpanzee — the more familiar common chimpanzee and
the pygmy chimpanzee or bonobo, *Pan paniscus*. The name “pygmy” is not an
accurate description of *Pan paniscus*. Pygmy chimpanzees are not smaller than the
best-studied subspecies of common chimpanzee, *P. troglodytes schweinfurthii*.
Pygmy chimpanzee males weigh approximately 45 kilograms, with a range that
extends from 40 to 60 kilograms for a large male. Females weigh less, averaging 33
kilograms with a range from 30 to 40 kilograms (Jungers and Susman, 1984).

Between July 1983 and July 1985, I spent a total of 20 months in central Zaire at
the Lomako Forest Pygmy Chimpanzee Project field site. The Lomako site trail
system covers an area of about 40 square kilometers of mainly climax evergreen forest
(White, 1986). The major part of the study site is high, polyspecific evergreen forest.
This is tall forest with a canopy of 30 to 40 meters, with large emergents reaching 60
meters. The forest is dissected by many small streams, each of which is flanked by an
area of low swamp forest and then a characteristic slope forest. There are areas of
second growth that represent areas cut in the 1920s, and they are typically low and
contain high densities of the tangled form of *Haumania* vine. The pygmy chimpanzees
eat the center of these vines on the ground, but otherwise the majority of their
food is fruit and young leaves.

We are able to recognize individual pygmy chimpanzees to varying degrees. The
easiest parameter to determine is the sex. Males are generally the hardest to tell apart
although there are differences in scrotum color. Females, when adult, often have
infants or juveniles with them, and their identification is aided by the idiosyncratic
nature of the sexual swellings. We can often recognize individuals by their faces,
many of which are very distinctive. Some animals even have deformed faces. These
are rare, and we do not know the exact cause in each case.

Our understanding of the social organization of this rare ape species is rapidly
increasing as the Lomako Forest study population gradually becomes more habituated to observers (White, 1988). This chapter presents a summary of recent studies of the social organization of the Lomako Forest pygmy chimpanzees, and makes some direct comparisons with the social organization of the common chimpanzees. This chapter also discusses recent work on the possible ecological correlates of the major differences in the social organizations of the common and pygmy chimpanzee.

SOCIAL ORGANIZATION

There are many features of an animal's social organization. The most commonly considered aspects are the observed social interactions and the way individuals associate in groups or parties. Social organization can also be determined from the way individuals associate in parties while feeding, as measured by their nearest neighbor choice.

Social Structure and Observed Interactions

Studies of social organizations ultimately depend on observations of the way in which individuals interact in a social situation. The different interactions between two individuals reflect their relationship to each other, and the social structure of sets of individuals is characterized by the context, quality, and patterning of the constituent relationships (Hinde, 1976, 1979).

The diverse social structures of primates in general, and great apes in particular, can be described by the distribution of interactions between the various age and sex classes. Thus, common chimpanzee social organization is typified by frequent affiliative behavior between males compared to infrequent affiliations among females (Goodall, 1968; Sugiyama, 1968; Nishida, 1979; Pusey, 1979). Gorillas display close relationships between the leading male and the females of a group, but not between the females themselves (Harcourt, 1979a, 1979b, 1979c). Orangutans are notable for the infrequency of any social interactions (Galdikas, 1979; MacKinnon, 1979; Rodman, 1979). The orangutan is essentially solitary (MacKinnon, 1974). Females do not maintain exclusive territories but have different, overlapping feeding ranges (MacKinnon, 1979). Resident males, in contrast, maintain exclusive territories that they defend from other males and that contain the feeding ranges of several females (Rodman, 1973, 1979). Affiliative behaviors within both males and females are rare, and there is a strong intolerance among males (Galdikas, 1979; Horr, 1975; MacKinnon, 1974; Rijksen, 1978; Rodman, 1973).

The African apes, however, are often found in larger social groupings. Gorillas live in cohesive groups that consist of a dominant male, a number of other adult males, adult females, and immatures (Schaller, 1963). As in the common chimpanzee and orangutan, affiliative behaviors between gorilla females are rare (Harcourt, 1979b), as are those between gorilla males (Fossey, 1974; Fossey and Harcourt, 1977). Gorilla groups maintain their cohesiveness despite the lack of interaction within the sexes because of the affiliation between each adult female and the dominant male of the group (Harcourt, 1979a, 1979b, 1979c).
Table 1. Social systems of apes.

<table>
<thead>
<tr>
<th>Species</th>
<th>Males</th>
<th>Females</th>
<th>Social system</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gibbon</td>
<td>no</td>
<td>no</td>
<td>monogamous</td>
</tr>
<tr>
<td>Orangutan</td>
<td>no</td>
<td>no</td>
<td>noya groups</td>
</tr>
<tr>
<td>Gorilla</td>
<td>no</td>
<td>no</td>
<td>communities</td>
</tr>
<tr>
<td>Common chimpanzee</td>
<td>yes</td>
<td>no</td>
<td>communities</td>
</tr>
<tr>
<td>Pygmy chimpanzee</td>
<td>no</td>
<td>yes</td>
<td>communities</td>
</tr>
</tbody>
</table>

*Note: Noyau social systems are based on separate but overlapping home ranges for each individual.*

Common chimpanzee females also rarely show affiliation toward each other (Bygott, 1979). Female common chimpanzees, with their young, live their lives in different, overlapping core areas (Halperin, 1979; Wrangham, 1975, 1979a, 1979b). Unlike gorilla males, however, common chimpanzee males are gregarious and cooperate to defend communal ranges that include the feeding ranges of several females (Goodall et al., 1979; Nishida, 1979). Males, in contrast, frequently show affiliative behavior toward other males and often groom each other (Goodall, 1968).

Preliminary observations on the pygmy chimpanzees of the Lomako Forest (Badrian et al., 1981) and at Wamba (Kano, 1980, 1982; Kuroda, 1979) have shown that pygmy chimpanzees, like common chimpanzees, display a fission-fusion social system in which individuals are found in parties that are flexible in size and composition. These individuals belong to geographically distinct associations or communities. Unlike common chimpanzees, affiliative behaviors between female pygmy chimpanzees are common. More recent work has supported this picture and expanded the affiliative behaviors to include food sharing between females (Badrian and Badrian, 1984; Kuroda, 1984). It has also become apparent that there is a unique behavior of genito-genital (GG) rubbing (Thompson-Handler et al., 1984) that is a mutual homosexual behavior between females.

Each ape, therefore, has a different social structure as reflected by the different bonds between and within the sexes (Table 1). The orangutan, gorilla, and common chimpanzee are characterized by a lack of strong affiliative bonds between the individual females. In contrast, pygmy chimpanzees appear to have a very different social structure, with strong affiliative behaviors between individual females.

It is perhaps not unexpected that among the ape species, with their drastically different body sizes and adaptations to different habitats, there should be markedly dissimilar social systems. However, it is less clear why there should be a major difference between the comparably sized pygmy and common chimpanzees. It is also not clear why the pygmy chimpanzee, unlike all other apes, should appear to show strong affiliation between females.
Recent studies of social interactions among the Lomako Forest pygmy chimpanzees have confirmed these preliminary observations (White, 1986; White, in review). Interactions between individuals were classed as either affiliative or agonistic aggressive plus submissive behaviors (White, 1986; White, in review). Affiliative behaviors included grooming and GG-rubbing. Aggressive behaviors were mainly chases but could also include threats, displacements, pursuits, and fights. Interactions were classed according to the sexes of the individuals involved. If the social organization of the pygmy chimpanzees is described in terms of direct observations, affiliation was observed among females and between females and males, but not among males.

Affiliative interactions involving either two females or a male and a female were common, whereas affiliative interactions between two males were infrequent (Table 2a). Differences were not due to males and females interacting affiliatively at different rates. Males, however, showed higher rates of involvement in agonistic interactions than females (Table 2a).

However, pygmy chimpanzees display a fission-fusion social organization. Females spent more time in parties with other females, whereas males often left or joined parties as lone animals (White, 1988). The chance of observing an interaction was dependent both on the numbers of individuals observed during a sighting and on the length of that sighting. Since there are usually more females than males in a party (White, 1988), the chance of seeing an interaction involving two females is greater. It is possible, therefore, that the observed interactions reflected the way individuals associated in parties.

Each sex may also not interact at equivalent rates. An expected frequency of interaction, based on equivalent rates, can be calculated from the time spent observing individuals of either sex. By comparing this expected frequency to the observed frequency for each sex, it was possible to determine if the sexes interacted at equivalent rates.

Each interaction by a male or a female, however, could be with an individual of the same sex or the opposite sex. If individuals interacted at random, the distribution of interactions would have been dependent on the number of each sex present at each sighting and the duration of that sighting.

In each sighting, the chances of an individual interacting with another of the same sex can be expressed as:

\[
\frac{(\text{number of individuals of that sex present} - 1)}{(\text{total party size} - 1)}
\]

Similarly, the chances of an individual interacting with another of the opposite sex can be expressed as:

\[
\frac{(\text{number of individuals of that sex present})}{(\text{total party size} - 1)}
\]

If individuals interacted with each sex randomly, the expected number of interactions can be calculated from these chances and the duration of each sighting.
Frances J. White

Table 2a. Total number of observed dyad interactions and number of times each sex was observed interacting. Expected numbers are based on equal rates of interacting for each sex.

<table>
<thead>
<tr>
<th>DYADS</th>
<th>All Interactions Observed</th>
<th>Affiliative Interactions Observed</th>
<th>Agonistic Interactions Observed</th>
<th>Unclassified Interactions Observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>n</td>
<td>196</td>
<td>150</td>
<td>39</td>
<td>7</td>
</tr>
<tr>
<td>Male-male</td>
<td>24</td>
<td>12</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>Male-female</td>
<td>84</td>
<td>67</td>
<td>13</td>
<td>4</td>
</tr>
<tr>
<td>Female-female</td>
<td>88</td>
<td>71</td>
<td>14</td>
<td>3</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>INDIVIDUALS</th>
<th>Observed</th>
<th>Expected</th>
<th>Observed</th>
<th>Expected</th>
<th>Observed</th>
<th>Expected</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male</td>
<td>132</td>
<td>138.5</td>
<td>91</td>
<td>106.0</td>
<td>37</td>
<td>27.6</td>
</tr>
<tr>
<td>Female</td>
<td>260</td>
<td>254.5</td>
<td>209</td>
<td>194.0</td>
<td>41</td>
<td>50.6</td>
</tr>
<tr>
<td>p&lt;sup&gt;1&lt;/sup&gt;</td>
<td>n.s.</td>
<td>n.s.</td>
<td></td>
<td></td>
<td>&lt; 0.05</td>
<td></td>
</tr>
</tbody>
</table>

Source: White, in review.
Note: n.s. = not significant.
1. G test for Goodness of Fit; Sokal and Rohlf, 1981.

There are several significant differences between these expected and observed distributions, as well as many nonsignificant differences. Males and females interacted at equivalent rates except that males interacted aggressively more often than expected. Males interacted with females and other males in direct proportion to the presence of females in the party for all types of interactions, with one exception. They interacted aggressively with other males significantly more frequently than they should if such interaction were independent of sex (Table 2b). Females interacted more frequently with males and less frequently with females than expected overall or in affiliative interactions (Table 2b).

Therefore, both females and males interacted more with females because females remained in parties more than males. On the basis of the observed social interactions, the social structure of pygmy chimpanzees can, therefore, be classed as one with a high degree of affiliative behavior among females and between males and females, but not among males. This observed distribution of social interactions, however, appears to be dependent on which individuals form parties. Social interactions, therefore, appear to be reflecting the prior level of organization of party composition.

Party Compositions

Having demonstrated this relationship between the observed social interactions and the way in which individuals are associating in parties, it is necessary to look at the results of studies of party composition (White, 1988; White and Burgman, in review). In the Lomako Forest, there are three separate associations or communities of pygmy
Table 2b. Division of interactions among individuals of same or opposite sex. Expected interactions are based on equal chances of interacting with either sex, given observed party composition.

<table>
<thead>
<tr>
<th></th>
<th>All Interactions</th>
<th>Affiliative Interactions</th>
<th>Agonistic Interactions</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed</td>
<td>Expected</td>
<td>Observed</td>
</tr>
<tr>
<td>Male with:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>48</td>
<td>41</td>
<td>24</td>
</tr>
<tr>
<td>Female</td>
<td>84</td>
<td>91</td>
<td>67</td>
</tr>
<tr>
<td>p^n</td>
<td>n.s.</td>
<td></td>
<td>n.s.</td>
</tr>
<tr>
<td>Female with:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>84</td>
<td>60</td>
<td>67</td>
</tr>
<tr>
<td>Female</td>
<td>176</td>
<td>200</td>
<td>142</td>
</tr>
<tr>
<td>p^n</td>
<td>&lt; 0.001</td>
<td></td>
<td>&lt; 0.01</td>
</tr>
</tbody>
</table>

Source: White, in review.
Note: n.s. = not significant.
1. G test for Goodness of Fit; Sokal and Rohlf, 1981.

Chimpanzees. In this study, the 17 best-known individuals from the two large communities, called the Hedons and the Rangers, and the 8 consistent members of a small splinter group, known as the Blobs, are used. Of the adults in the Hedon community, 5 were males and 12 were females; of the Rangers, 7 were males and 10 were females. The Blobs consisted of 5 males and 5 females.

Parties of pygmy chimpanzees frequently undergo fission and fusion and thus maintain the same composition for varying lengths of time. It is possible to examine the associations among individuals that show a social organization of this type by using methods developed for Numerical Taxonomy (White, 1986; White and Burgman, in review). Each time the party composition changed by one or more individuals entering or leaving the party, a new record of the individuals present was made. This produced a matrix of the amount of time that individuals spent together in parties. This matrix was used to calculate the following index of similarity between individuals. The amount of time that Chimp 1 and Chimp 2 were present together in a party was divided by the total time that either one was present (Table 3). This is a quantitative analogue of Jaccard’s coefficient (standardized between 0 and 1) and gives a measure of the similarity between individuals based on the time that they spent together in parties.

Clustering was calculated using UPGMA (unweighted pair group method using arithmetic averages). The dendrograms of party composition were constructed separately for the two communities and the splinter group. The data from the Hedons were probably the most realistic as this group was the most habituated and was found in a
Table 3. Method of calculating association matrix for party composition.

<table>
<thead>
<tr>
<th>Number of minutes</th>
<th>Chimp 2 present</th>
<th>Chimp 2 absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chimp 1 present</td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Chimp 1 absent</td>
<td>c</td>
<td>d</td>
</tr>
</tbody>
</table>

Measure of similarity between individuals
(Quantitative analogue of Jaccard's coefficient)

\[
\frac{a}{a + b + c}
\]

Source: White and Burgman, in review.

Figure 1. Hedon community. Dendrogram of relative time spent together.

Figure 2. Hedon community. PCA of relative time spent together.

Source: White and Burgman, in review.

Note: Proportion of variance explained by axes 1 to 4 = 0.717
♀ = female    ♂ = male    e = mother

Source: Adapted from White and Burgman, in review.
♀ = female    ♂ = male
wide range of party sizes. The Blobs, as a small splinter group, were confined to showing only small party sizes, and the Rangers were only observed in superabundant food sources and, as party size is related to the size of the food patch (White, 1986; White and Wrangham, 1988), the Rangers always showed unusually large party sizes. These differences are important, as they were reflected in the different structuring of the data. That is, there are different effects when parties are unusually large, whereas having only small party sizes tends to emphasize greatly the underlying structuring in the party composition data.

In the Hedon dendograms there are subgroups that cluster together (Fig. 1). These subgroups are either males with females, or females with other females. Another way of looking at this same data is by Principal Components Analysis (PCA). The plot of the first two axes (Fig. 2) shows that females fall into two clusters, whereas there are no clusters of males. The dendrogram of the Rangers shows less higher-order structure, but there are still subgroups of males plus females (Fig. 3). The first two axes in this case, however, show an almost random distribution of points (Fig. 4). The

Figure 3. Ranger community. Dendrogram of relative time spent together.

Figure 4. Ranger community. PCA of relative time spent together.

Source: Adapted from White and Burgman. in review.

\( \bullet \) = female \( \square \) = male

Source: White and Burgman, in review.

Note: Proportion of variance explained by axes 1 to 4 = 0.677

= female \( \checkmark \) = male \( \bigcirc \) = mother
Blobs have a cluster of females (Fig. 5), and the PCA plot shows linked females and more loosely associated males (Fig. 6). White and Burgman (in review) show that the female cluster is tight and that there is a clear progression from tightly linked females to more loosely linked males.

It is possible to test whether the structure that one observes in data of this type is due to particular factors. This is done with a Mantel test, with significance based on a Monte Carlo simulation of the data (Schnell et al., 1985). The most significant factor in the structure of the party composition data in the Hedons and the Blobs is associations between females (Table 4). However, in the Ranger data, the structure is more dependent on male-female and male-male associations.

**Nearest Neighbors**

A similar analysis can also be done for feeding proximity data (White, 1986; White and Burgman, in review). The nearest neighbor's identity and distance to a focal animal was recorded at two-minute time points. In this analysis, 5 meters was used as a measure of proximity, as behavioral data have shown that this is the approximate distance of an individual's feeding sphere. The amount of time that individuals spent
within 5 meters of each other was converted into a similarity association matrix like that for party composition data. The measure of similarity between individuals was:

\[
\frac{X_{i,j} + X_{j,i}}{n_i + n_j}
\]

where:
- \(X_{i,j}\) is the frequency that \(i\) was the nearest neighbor within 5 meters of \(j\).
- \(X_{j,i}\) is the frequency that \(j\) was the nearest neighbor within 5 meters of \(i\).
- \(n_i\) is the frequency that \(i\) and \(j\) were focal animals.

This value, therefore, reflected the time that any two individuals were close together as a proportion of the amount of time that either of them was the focal animal being sampled.

The results from Mantel tests on these data (Table 5) were very similar to the results from the Mantel tests of party composition. The structure in the Hedon and

<table>
<thead>
<tr>
<th>Table 4. Mantel tests of party composition data.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Community</td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Female-female</td>
</tr>
<tr>
<td>Hedons</td>
</tr>
<tr>
<td>0.714</td>
</tr>
<tr>
<td>Male-male</td>
</tr>
<tr>
<td>0.286</td>
</tr>
<tr>
<td>Male-female</td>
</tr>
<tr>
<td>0.300</td>
</tr>
</tbody>
</table>

*Source: White and Burgman, in review.*

Table 5. Mantel tests of feeding proximity data.

<table>
<thead>
<tr>
<th>Community</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hedons</td>
</tr>
<tr>
<td>Female-female</td>
</tr>
<tr>
<td>Male-male</td>
</tr>
<tr>
<td>Male-female</td>
</tr>
</tbody>
</table>

*Source: White and Burgman, in review.*

* Denotes significance of \(p < 0.05\).*
Blobs data was strongly influenced (in the Blobs, it is statistically significant) by associations between females. In the Rangers, however, the major effect was a male-female association, and there was no male-male effect. This, when taken together with the results from the Mantel test of party compositions, could be an indication that the Ranger males were attracted into the unusually large parties observed, but they entered the parties in order to maintain proximity to females.

In summary, therefore, data on interactions, party composition, and nearest neighbors all indicate that the social organization of pygmy chimpanzees can best be categorized as one in which there is strong affiliation among females and between males and females, but not among males.

ECOLOGICAL CORRELATES OF THE SOCIAL ORGANIZATION

The social organization of pygmy chimpanzees can, therefore, be considered as female-based. This is very different from the male-bonded social system of common chimpanzees. Wrangham (1979a, 1979b) has hypothesized that, since their food occurs in small patches, the high cost of feeding competition prohibits sociality among female common chimpanzees. In a recent comparison of food patches of pygmy and common chimpanzees (White and Wrangham, 1988), it was found that pygmy chimpanzees feed more frequently in large trees than do common chimpanzees (Table 6). Pygmy chimpanzees visit larger patches than common chimpanzees do (Table 7). Feeding competition is, therefore, presumably less in the pygmy chimpanzee. Females can thus afford to associate with other females.

<table>
<thead>
<tr>
<th>Patch type</th>
<th>Pan paniscus</th>
<th>Pan troglodytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ground (leaves + pith)</td>
<td>14.3</td>
<td>16.2</td>
</tr>
<tr>
<td>Ground (insects)</td>
<td>0.0</td>
<td>2.7</td>
</tr>
<tr>
<td>Vines</td>
<td>4.9</td>
<td>17.3</td>
</tr>
<tr>
<td>Small trees</td>
<td>15.6</td>
<td>24.9</td>
</tr>
<tr>
<td>Large trees</td>
<td>64.8</td>
<td>38.9</td>
</tr>
</tbody>
</table>

Note: G test value = 28.36, p < 0.005.
Table 7. Frequency distribution of patch sizes (percent of all patches).

<table>
<thead>
<tr>
<th>Patch size estimate (number of chimp-minutes)</th>
<th>Pan paniscus</th>
<th>Pan tragledytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 to 50</td>
<td>38.8</td>
<td>59.1</td>
</tr>
<tr>
<td>50 to 100</td>
<td>14.7</td>
<td>19.4</td>
</tr>
<tr>
<td>100 to 150</td>
<td>5.4</td>
<td>10.8</td>
</tr>
<tr>
<td>150 to 200</td>
<td>7.0</td>
<td>4.3</td>
</tr>
<tr>
<td>200 to 250</td>
<td>6.2</td>
<td>2.7</td>
</tr>
<tr>
<td>above 250</td>
<td>27.9</td>
<td>3.7</td>
</tr>
</tbody>
</table>

Note: Kruskal-Wallis H value = 15.19, p < 0.005.

ACKNOWLEDGMENTS

I would like to thank John Fleagle for his continuing advice and guidance and Randall Susman and Noel Badrian for introducing me to the pygmy chimpanzees of the Lomako Forest. Many of the results presented here are from productive collaborations with Richard Wrangham and Mark Burgman. I would especially like to thank Nancy Thompson-Handler and Richard Malenky, as it is thanks to them that my time in the forest was both enjoyable and highly productive. This work owes much to the comments and suggestions of Charlie Janson, Mark Burgman, and Richard Wrangham. I would also like to thank Donald Gerhart for all his help and for suggesting the use of techniques from phenetics for analysis of association data, Gary Schnell for suggesting the Mantel test, and Scott Ferson for computer assistance. This work was supported by a NSF Doctoral Dissertation Improvement Award and a grant from the Boise Fund.

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