INTRODUCTION

*Pan paniscus*, the pygmy chimpanzee or bonobo, has been studied at a number of sites in Zaire including Lomako, Wamba, Ikela, and briefly at Yalosidu and Lake Tumba. Lake Tumba (Horn, 1980) is a swamplike habitat that is visited by pygmy chimpanzees only seasonally. Studies in the mosaic of undisturbed, disturbed and swamp forest of Yalosidu (Kano, 1983; Uehara, 1988, 1990) and at Ikela in the Lilungu region (Sabater Pi *et al.*, 1993) have yet to yield detailed results on socio-ecology. In contrast, investigations at Lomako Forest (Badrian & Badrian, 1984; Badrian & Malenky, 1984; Thompson-Handler *et al.*, 1984; White, 1985, 1988, 1989a, 1989b, 1992a, 1992b; Malenky, 1990; Thompson-Handler, 1990; White and Burgman, 1990; White & Lanjouw, 1992; Hohmann & Fruth, 1993, 1994; Fruth & Hohmann, 1994, Chapter 17) and at Wamba (Kuroda, 1979, 1980, 1984; Kano, 1980, 1982, Chapter 10; Kitamura, 1983; Kano & Mulavwa, 1984; Furuiuchi, 1987, 1989, 1992; Idani, 1990, 1991; Ihobe, 1992a, 1992b) have both spanned several years and have provided much of the information currently available on the behavior of the pygmy chimpanzee, so that most of the comparisons presented here concentrate on the differences and similarities between the Lomako and Wamba study populations. There are differences in methods used and in the type of information available from each site. Provisioning at Wamba has facilitated habituation, so that more detailed behavioral data collection is possible. Studies at Lomako have emphasized long-term observation without provisioning.

As for many social species, the social organization of bonobos can be correlated with several ecological variables. Such relationships can be useful in explaining both the variation within the species as well as the divergence of the bonobo from other apes, especially the closely related chimpanzee, *Pan troglodytes*. It is also possible to examine specific behavioral patterns from a similar socio-ecological perspective. Some such behaviors highlight the relative differences between bonobos and chimpanzees, such as food sharing and inter-party coordination and communication, whereas others can be considered as truly unique adaptive strategies of the bonobo: one of the most obvious of these is genito-genital rubbing among females.

Like chimpanzees, bonobos share both plant and animal foods (Kuroda, 1984; Ihobe, 1992b; Hohmann & Fruth, 1993; White, 1994). Unlike chimpanzees, there is no evidence to date that bonobos actively hunt mammalian prey, as observations indicate that prey species such as squirrels (*Uromastyx* sp.) and duikers (*Cephalophus nigerfrons*, *Cephalophus dorsalis*) are taken only opportunistically as encountered. Once obtained, meat appears to be a highly-prized food item, given the relatively high frequency of begging and the low rate of sharing. Unlike chimpanzees, however, female bonobos can retain ownership of meat even from adult males, and male–male sharing is rare. Meat sharing is not consistent with the sharing-under-pressure hypothesis (Wrangham, 1975) that may explain meat sharing in chimpanzees, possibly because bonobos have weaker male–male bonds and bonobo females can cooperatively dominate males (Kano, 1992; Parish, 1994). As in chimpanzees, plant foods are shared between bonobo mothers and infants, but unlike chimpanzees, there is frequent sharing between adult bonobos, especially among females and between females and males, with females sharing more

[29]
frequently than males. The occurrence of plant food sharing may be related to the relatively large fruits available in the bonobo habitat, including such fruits as *Treculia africana*, a single fruit of which can weigh 10–20 kg. Food sharing patterns appear to be consistent with ideas of reciprocal sharing (Trivers, 1971; de Waal, 1989), where the return currency may be equivalent sharing or, in the case of male–female sharing, future sexual access or food sharing to gain status (Moore, 1984).

Like chimpanzees, bonobos have a fission–fusion social organization in which individuals within a community associate in groups of variable size and composition. There seem to be real differences between the species, however, in intercommunity relationships (see below). Bonobo parties also change less frequently than chimpanzee parties at Tai (Boesch, Chapter 8) and at Gombe (Halperin, 1979), but not those at Bossou (Sugiyama, 1984). Parties of bonobos are mostly mixed in composition, containing both male and female adults and lower frequencies of groups of mothers (Boesch, Chapter 8), although all-female parties of females with or without offspring can be highly stable (White, 1988). Lone individuals are relatively rare, and unlike most chimpanzee populations, are usually males (White, 1988). There seem to be only quantitative differences between chimpanzees and bonobos in the way parties split and coalesce, especially when feeding (Chapman et al., 1994). During periods of fruit abundance where several trees are in fruit in a given area, bonobos seem to be more cohesive, remaining together to visit the same large trees, whereas chimpanzees disperse among many neighboring trees. A similar difference has been seen within a single tree, where chimpanzees disperse while feeding so that nearest-neighbor distances increase with the size of the food tree (Ghiglieri, 1984), while bonobos remain more bunched, so that the size of the canopy explains relatively little variation in nearest-neighbor distances during feeding (White, 1986). Differences also exist in the cohesiveness of the sexes during feeding, with male–male spatial cohesion in chimpanzees versus male–male dispersion in bonobos (White & Chapman, 1994). Bonobo parties also seem to congregate at night to form larger sleeping parties (Furuichi, 1989; Fruth & Hohmann, 1994). Unlike chimpanzees, parties of bonobos seem not to comprise females meeting within their separate but overlapping core areas, since non-

estrous female bonobo core areas can be as large or larger than those of males (White & Lanjouw, 1992).

The vocalizations of Lomako's bonobos are very different from chimpanzee vocalizations (Hohmann & Fruth, 1994) and appear to be important in inter-party communication. Bonobo long calls do not appear to be suitable for long distance communication (de Waal, 1988; Hohmann & Fruth, 1994) and are only detectable in the Lomako Forest within about 500 m. The structure of these calls, however, may allow more precise detection of location (Hohmann & Fruth, 1994), thus allowing for coordination of separate parties. Vocalization rates vary during the day, with late afternoon vocalizations being associated with travel and occupation of nests, whereas morning vocalizations are associated with movements between and arrival at feeding sites (Hohmann & Fruth, 1994). These peaks of vocalizing in the morning correspond to peaks in feeding activity (White, 1986).

Genito-genital or GG rubbing is an affiliative behavioral pattern of female bonobos. Usually two, but sometimes more, females clasp each other ventrally and rapidly rub the anterior surface of the external genitalia together with a repeated lateral motion. Associations between GG rubbing and feeding have been seen in the wild (Kano, 1980; Kuroda, 1980; Thompson-Handler et al., 1984; White, 1986; White & Lanjouw, 1992) and in captivity (de Waal, 1987). GG rubbing seems to ease tension during group excitement (de Waal, 1987) and is associated with begging for food and heterosexual matings (Kuroda, 1984; Thompson-Handler et al., 1984). GG rubbing occurs in situations of reduced feeding competition (White & Lanjouw, 1992) and may reflect cooperative alliances among females for food patch defense (White, 1986; White & Lanjouw, 1992).

Although a number of features of the bonobo social system are consistent between Lomako and Wamba, several important differences demonstrate the variability of *Pan paniscus*. Most studies at Wamba have concentrated on social behavior (e.g. Kano, 1992) with most ecological work being done at Lomako (e.g. Malenky, 1990; White, 1992a). It is, therefore, not always possible to relate intersite differences to ecological differences. However, variation in some aspects of social organization can be related to variability within one site, and can be expanded to offer possible explanations for differences between sites. This chapter examines some issues that
have not been documented at more than one site or that show intersite variation, and it attempts to relate these differences to ecological differences whenever possible.

There are both major differences and similarities in social organization between chimpanzees and bonobos. Female bonobos are more cohesive and affiliative with each other than are female chimpanzees, and the degree of male bonding observed in chimpanzees is not seen in bonobos. The greater sociality of female bonobos can be related to reduced feeding competition in this species. This reduced competition both allows bonobo females to be more social, and provides further benefits to females in the cooperative defense of food patches against other community members as well as other communities. It has been suggested that defense of food patches is mediated through interparty vocalizations (White, 1986), which may relate to the correspondence between peaks in vocalizations and morning feeding. Lower feeding competition in bonobos may be due to more than one factor, including the abundance, size and distribution of fruit trees, and the use of terrestrial herbaceous vegetation (THV). The differences in food patch utilization between species is complex and is discussed in more detail below, while the importance of THV is discussed by Wrangham et al. (Chapter 4).

METHODS

The data came from the Lomako Forest study site in the Province of Equateur in central Zaire. Situated at 0° 51’ N 21° 5’ E, the site consisted of about 40 km² of a mosaic of forest types, principally climax, evergreen, polyspecific rain-forest, with some areas of secondary growth, slope and swamp forest (White, 1992a). The study subjects used all types of forest, but spent most of their time in the undisturbed climax forest (93% of focal animal sampling: White, 1992a). Parties were found by vocalizations, walking trails, vigil at fruit-trees and prior knowledge of location. Nest-to-nest follows were conducted whenever possible. Focal sampling started when individuals left their overnight nests in the morning and stopped when they settled in their overnight nests in the evening. Nests were then watched for at least 30 minutes. Parties were defined as all individuals in a behaviorally cohesive unit that maintained visual contact and coordinated movements and activities. Individuals within the same party were often separated by as much as 100 meters in the trees. Changes in party size tended to be obvious, due to the extensive vocal and social exchanges between members of merging parties. Party fission was often harder to determine, since large parties would often rest dispersed throughout several trees. A change in party membership was considered to have occurred if a departure was observed, or if all previous members of the party could not be found by the observer and did not appear when the remaining party members reunited to eat or to travel. Party size was recorded at each 2- or 5-minute time-point (see below) and mean hourly party sizes were extracted from the data using only time-points that fell on the hour.

Individual recognition was based on distinctive characteristics and facial features. All individuals were classed by age, sex, and state of perineal swelling as described elsewhere (White, 1986). Data are presented from 2-minute focal subject sampling from October 1984 to July 1985 on the Rangers (Eyengo) and Hedon communities and on the Blob splinter group, and from 5-minute focal subject sampling from June to August 1991 on the Rangers and Hedon communities. The Blobs ceased to exist as a distinct unit by 1991. Interactions were recorded opportunistically. Dominance rank among individuals was determined using decisive agonistic interactions such as a dominant chasing a retreating subordinate. Observation time totaled 406.4 hours.

The nearest neighbor of the focal subject was recorded at each time-point and used to construct an association index based on relative time spent together (White & Burgman, 1990). These data were used to look for significant association patterns using Mantel (1967) tests as described below (see section on Community residence and the influence of mother-son bonds). As the data used did not conform to the assumptions of parametric tests, non-parametric statistical tests (Sokal & Rohlf, 1995) were used throughout.

RESULTS

Female-female versus male-female affiliation

There are differences in social organization between study sites (Kuroda, 1979; Kano, 1982; Kitamura, 1983; Badrian & Badrian, 1984; White, 1988, 1992b). At
Wamba, there is frequent affiliation between males and females in many aspects of social organization, including interactions and relationships (Kano, 1980; Kuroda, 1980, 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 documented (Kano, personal communication in Nishida & Hira-iwa-Hasegawa, 1987; Furuichi, 1989) and may be an important influence on the social status of males (Furuichi, 1989; Ihohe, 1992a). Studies at Wamba have found association, if not affiliation, among females, but this is generally thought to be secondary in importance to affiliation between the sexes (Kano, 1982; Kitamura, 1983; Furuichi, 1989).

Studies of the Lomako Forest population have also found a high degree of affiliation between males and females and among males, but not among males (Badrian & Badrian, 1984; White, 1988, 1989b, 1992b; White & Burgman, 1990). Studies of party membership, however, have shown associations among females as being more significant than associations between males and females (White, 1986; White & Burgman, 1990). The two study sites, therefore, differ in the relative importance of affiliation between males and females compared with affiliation among females.

**Party size and affiliation rates**

This difference in patterns of affiliation may be related to differences in party size between the sites (White, 1992b). At Lomako, patterns of interactions varied with party size and composition. Female–female affiliation predominated in small parties (2–6 individuals), while male–female affiliation was more common in intermediate (7–10) and large (11 or more) parties (White, 1992b; see Fig. 3.1). The monthly rate of affiliation among and between the sexes was calculated from the number of observed interactions divided by the number of focal subject time-points for that month. As some months had only female–female or male–female affiliation, bimonthly means were used to pool data and to avoid zeros in ratio calculations. The bimonthly rate of male–female affiliation increased with party size (Spearman correlation coefficient, \( r_s = 0.97, N = 5, p < 0.005 \)), whereas the rate of female–female affiliation did not \( (r_s = 0.20, N = 5, ns) \). As Lomako parties increase in size, there is more male–female affiliation relative to female–female affiliation. This pattern is similar to nearest neighbor and party membership association patterns found at Lomako (White & Burgman, 1990), where there is significant female–female affiliation in small parties, but at larger party sizes males join to maintain proximity with females.

Party sizes at Wamba are considerably larger than those at Lomako (see Table 3.1). Counts of party sizes are available for both sites and show that party size has varied somewhat more at Wamba than at Lomako. Means for party size based on focal subject sampling at Lomako yield larger party sizes than their corresponding means from counts (Wilcoxon two-sample test \( U_s = 467989, r_s = -5.09, p < 0.001 \)), since larger parties remain stable longer than smaller parties (Kendall’s coefficient of rank correlation, party duration vs. party size, \( \tau = 0.33, N = 164, p < 0.001 \)). If the same variation in affiliation patterns observed at Lomako also occurs at Wamba, the differences in male–female to female–female affiliation may simply reflect larger party sizes at Wamba.

**Variation in party size**

At Lomako, party size varies with the dimensions of the food patch, measured as the radius of a tree or vine canopy (White, 1986; White & Wrangham, 1988). Small patches (of less than 10 m radius) contain limited amounts of food and feeding competition is high. Larger patches (of greater than 10 m radius) contain superabundant food and there is little or no apparent feeding competition (White & Wrangham, 1988). Larger parties, therefore, occur in large superabundant food patches. Some measures of affiliation can be directly related to measures of feeding competition, such as the rate of GG rubbing between females, which, although not correlated with the size of parties, is inversely correlated with the rate of feeding competition (White, 1986; White & Lajanouw, 1992).

The size and abundance of food patches varies throughout the year. At Lomako, party size varied monthly (Kruskal–Wallis test, differences in mean party size over ten months, measured at hourly time points, \( H = 77.86, df = 9, p < 0.0001 \)). Party size is lowest
during the months of October and November. This is about the period of lowest fruit production at Lomako, which occurs November through December (Malenky, 1990). This party size variation is significantly correlated with the average size (as measured by patch radius) of food patches used each month ($r_s = 0.64$, $N = 10$, $p < 0.05$, see Fig. 3.2).

Differences in party size between Wamba and Lomako may reflect differences in patch size, possibly because one effect of provisioning is to provide a consistent, large food patch. Differences in party size are not consistent with differences due to habituation, since party sizes at Lomako have decreased with habituation therefore producing greater differences between the sites. Differences in non-human predation pressure also do not reflect intersite differences, as party size is expected to increase with predation threat. Parties at Lomako, where predators are common, are smaller than
Fig. 3.2. At Lomako, mean monthly party size and mean monthly food patch radius (1984-85 data only). Party size means are calculated from party size recorded at hourly time-points and averaged by calendar month. Monthly food patch radii are

at Wamba, where such predators are locally extinct.

Inter-site differences may be due to pressures from human populations, as Wamba is more densely populated and has extensive habitat disturbance, whereas Lomako is not (White, 1992b; Appendix).

**Fission–fusion**

The fission–fusion social system of pygmy chimpanzees is characterized by temporary associations or parties. At Lomako, parties fission and fuse so that members of the same community may be separated by kilometers for days or weeks. All members of one community at Lomako have yet to be seen in one place at the same time. In contrast, at Wamba, there appears to be less fission and fusion, although it is hard to make comparisons due to differences in the methods of defining parties. At Wamba, individuals that traveled separately but maintained vocal contact were considered to be members of the same party (Kano, personal communication). Under the definition for the Lomako data used here, these loners would have been considered as separate parties. However, despite these difficulties, some differences remain. All members of the E1 community at Wamba usually formed one mixed party consisting of most of its members (Furuichi, 1989). Although this community fragmented during the day, they coalesced back into a single party to sleep at night. At Lomako, occasional gatherings of larger parties were observed to come together to nest, and hourly party size in the late afternoon to evening (15.00–18.00 hours) were significantly larger (2.5 individuals excluding infants) than those earlier (05.00–14.00 hours, mean party size = 6.8 individuals excluding infants) in the day (Fig. 3.3: Kruskal–Wallis $H = 6.59, df = 1, p < 0.02$).

There are no data available on food patches at Wamba. Since party size varies with the size of food patch at Lomako, the reduced rates of fission and fusion

from counts of individual patches visited by month and include repeated visits to the same food tree. Means and one standard error are plotted for each month.
at Wamba may simply reflect the larger party size selected for by provisioning, so that the pygmy chimpanzees no longer need to range widely in small parties to utilize efficiently small patches, but rather they have switched to a strategy of closer association for feeding in the artificial feeding site or when food is provided by observers in the forest. However, larger parties recorded by Kuroda (1979) were seen before provisioning was successful. Alternatively, these larger parties may be an adaptation to the greater predation pressure from local human populations at Wamba or from other impacts of the local humans, such as removal of forest resources or introduction of food crop species into areas used by the bonobos.

**Intercommunity association and female transfer**

At both Lomako and Wamba, peaceful associations between members of different communities have sometimes been seen (Idani, 1990, 1991; Thompson-Handler, 1990; Doran, personal communication; personal observations). However, due to the lack of fission-fusion at Wamba, such aggregations appear to be the whole of two communities coming together most often at the artificial feeding site (Idani, 1990), whereas at Lomako these associations usually consist of only a few individuals of each community. During these associations at Wamba, young nulliparous females were seen to move between communities (Idani, 1990, 1991). At Lomako female transfer has also been observed. A splinter group known as the ‘Blobs’ that included two nulliparous females was seen as distinct from the other two communities from 1984 to 1985 (White, 1988); but by 1991 these two females had become parous females within the Hedon community and at least one of the Blob males was also observed in the Hedon community. Similarly, in the Ranger community, two highly peripheral nulliparous females were seen in 1984–85 occasionally...
associating with community members, and by 1991 one of them was a central parous female within the Ranger community.

**Community residence and the influence of mother-son bonds**

Since females transfer between communities, adult females within a community are unlikely to be related. Males, in contrast, appear to remain in their natal community (Kano, 1982; Furuichi, 1989). At Lomako, at least one juvenile male has risen to mating status within his community. At Wamba, the dominance rankings of adult males are strongly influenced by the presence of their mothers in the community (Furuichi, 1989; Ihobe, 1992a). At both Wamba and Lomako, old females occupy the highest ranks among the females (Furuichi, 1989; personal observations), but strong ties between old females and adult sons have yet to be demonstrated at Lomako.

It is possible to test for the statistical significance of such affiliations by using an association index that incorporates the time two individuals spend as nearest neighbors in parties (White & Burgman, 1990). The observed association indices for two communities and the splinter group for 1984–85 data were tested against two hypothetical matrices using a Mantel test (Mantel, 1967; Schnell et al., 1985). The hypothetical matrices tested were for important affiliations: (1) between old females and other adult females; and (2) between old adult females and adult males. This yields a Mantel test statistic, $Z$, that can be compared to its permutational distribution (see White & Burgman, 1990). For this test, 5000 random permutations were used.

While there were no significant associations between old females and other females in either community or in the splinter group, there was a significant association between old females and adult males in one community (Hedons; $Z = 0.29$, $p = 0.003$) but not in the other community (Rangers; $Z = 0.05$, $p = 0.236$). In the Hedon community, the males in association with old females did not include, however, the highest-ranking (alpha) male (Fig. 3.4). Thus, the evidence at Lomako of bonds between old females and adult males may represent bonds between mothers and their sons. This hypothesis may be tested in the future using DNA fingerprinting to determine interindividual relationships.

**Relatedness and dominance hierarchies within communities**

Paradoxically, communities of pygmy chimpanzees seem to be composed of unrelated females who are highly affiliative with each other (Fig. 3.5) and of related males who are not highly affiliative with each other. There is a dominance hierarchy among males at Wamba with a single dominant male and with adults outranking adolescents (Furuichi, 1991; Ihobe 1992a). At Lomako the top-ranking male in each community and in the splinter group was clear, based on a small sample of decisive aggressive interactions, but relative rankings among the other males were not obvious. In the Hedon and Ranger communities and in the Blob splinter group, the top-ranking male evicted or excluded other males from feeding trees at the start of feeding bouts when most matings occurred, and one of the dominant males interrupted mating attempts by other males. Adult male pygmy chimpanzees outrank adult females in that males will occasionally aggress against females, but females often ignore such male pressure. For example, unlike *Pan troglodytes*, female *Pan paniscus* at Lomako can retain a duiker carcass and not be forced to share it with begging males (White, 1994). Therefore, pygmy chimpanzees present a unique complex among apes of what is essentially female-bonding without female kinship, male kinship without male-bonding and relatively little ability of males to dominate females.

**Comparison of socio-ecology in *Pan paniscus* and *Pan troglodytes***

Earlier examinations of the differences in social organization of chimpanzees and pygmy chimpanzees supported the hypothesis that pygmy chimpanzees have a reduced level of feeding competition that permits the larger parties observed in pygmy chimpanzees (White, 1986; White & Wrangham, 1988). The level of feeding competition in trees shown by Lomako's pygmy chimpanzees was found to be lower than that for Gombe chimpanzees (White & Wrangham, 1988), supporting the hypothesis that bigger food trees for pygmy chimpanzees may permit greater female sociality. However, in a recent test of these ecological parameters for rain forest chimpanzees at Kibale, Chapman et al. (1994) found that
Kibale chimpanzees used patch sizes that were comparable to those at Lomako, although female–female affiliation at Kibale was similar to other populations of *Pan troglodytes* (Wrangham et al., 1992). However, the relationship between patch size and feeding competition differed between the two species, in that the amount of food removed from large patches at Kibale was not dependent on the number of individuals present. 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) concluded that variation in the levels of competition throughout the year may be the most important factor...
in determining interspecific differences in social bonding.

This interpretation is supported by comparisons of the variation in monthly mean party size. Party size for focal subjects was measured at each time-point (every 15 minutes for Wrangham et al., 1992, every 2 minutes for Lomako 1984–85 and every 5 minutes for Lomako 1991), as shown in Table 3.2. Mean party size was smaller for more months at Kibale than at Lomako ($G = 3.98$, $p < 0.05$). The party size measured by this method also showed larger mean party sizes overall for Pan paniscus than for P. troglodytes. These party size differences are not due to differences in community size, since Kibale communities are bigger than Lomako communities (Table 3.2).

As at Lomako, there was at Kibale a significant correlation between mean monthly party size and food abundance (Wrangham et al., 1992). These results imply that there is more variation in food and distribution for P. troglodytes than is experienced by P. paniscus, suggesting that it is the level of variation in food availability rather than the absolute amount that is the critical difference selecting for differences in social organization between the two species. This interpretation of the socioecological differences between the species is supported by observations for another population of rain forest chimpanzees studied at Tai Forest, where party sizes of chimpanzees are also highly variable (Boesch, personal communication) and where during periods of food shortages small parties are often observed (Doran, 1989).

**CONCLUSIONS**

The social organization of Pan paniscus with its female bonding among non-relatives is unique among non-human primates. Comparisons of the degree of female bonding in many aspects of social organization, including affiliative interactions, food sharing, GG rubbing, nearest neighbors and party composition, have shown variation that can be correlated with variation in feeding competition in food patches. Less feeding competition is correlated with more female–female affiliation. This close tie between female bonding and ecological parameters in P. paniscus, together with the ecological differences between P. paniscus and Pan troglodytes, suggest that the social differences between the two species can be related to greater variability in feeding competition experienced by P. troglodytes compared with the relatively more stable levels seen by P. paniscus. Unlike P. troglodytes, the sociality of P. paniscus females and the lack of core areas in their ranging (White & Lanjouw, 1992) mean that P. paniscus males cannot cooperate to defend the range of more than one female. Single P. paniscus males, in

<table>
<thead>
<tr>
<th></th>
<th>Mean monthly party size less than 5</th>
<th>Mean monthly party size greater than 5</th>
<th>Number of months sampled</th>
<th>Average party size variation</th>
<th>Community size (including infants)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kibale$^a$</td>
<td>66.6%</td>
<td>33.3%</td>
<td>18</td>
<td>5.6 to 6.1</td>
<td>37</td>
</tr>
<tr>
<td>Lomako$^a$</td>
<td>30.8%</td>
<td>69.2%</td>
<td>13</td>
<td>7.21 to 7.26</td>
<td>28, 35, 9</td>
</tr>
</tbody>
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Notes: $^a$Data from Wrangham et al., 1990.
$^a$Data from 1984–1985 and 1991 combined (Hedons, $^a$Rangers, $^a$Blobs).
contrast, are able to monopolize small cohesive groups of females and to exclude other males, so that in small parties there is typically only one male (Fig. 3.6). As party size increases, the proportion of males increases, as it is no longer possible for a single male to exclude others, so that in larger parties individual male–female relationships become more important.

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