

SOCIAL AND SPATIAL ASPECTS OF MALE SUBGROUPING IN A COMMUNITY OF WILD CHIMPANZEES

by

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Summary

Strong social bonds typically develop between dyadic pairs of male chimpanzees. These bonds are manifest in several contexts, including association, grooming, and proximity. Here we demonstrate that social bonds exist at a higher level of organization among males living in an extremely large community at Ngogo, Kibale National Park, Uganda. An analysis of over 2,500 hours of observation of 35 individuals revealed two distinct subgroups of male chimpanzees. Males that composed each subgroup can be identified on the basis of their tendency to associate in temporary parties. Matrix permutation tests indicated that subgroup members tended to maintain spatial proximity to each other and participate together in territorial boundary patrols. Subgroups formed along the lines of age and rank; members of a small subgroup were younger and lower ranking than individuals in a larger subgroup. Despite this social clustering of males, community integrity remained intact with low levels of aggression between individuals of different subgroups. After controlling for the effect of association, significantly more aggression occurred within compared to between subgroups. In addition,

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males of the different subgroups displayed significant overlap in their use of the community territory and thus showed no tendency to divide spatially. We compare our findings with those from other animal species and chimpanzee populations and discuss them in the context of the unusual demography of the Ngogo community.

Introduction

The analysis of animal social systems is a central focus of ethological research (Rubenstein & Wrangham, 1986; Smuts *et al.*, 1987; Brown & Brown, 1996; Mann *et al.*, 2000). Describing animal societies and elucidating the factors underlying their structure and organization represent fundamental challenges (Clutton-Brock, 1989; Pepper *et al.*, 1999; Whitehead & Dufault, 1999; Kappeler & van Schaik, 2002).

Wild chimpanzees furnish a model system for the analysis of animal societies. Chimpanzees live in communities or 'unit groups,' whose members associate in temporary parties that vary in size and composition (Nishida, 1968; Goodall, 1986; Boesch & Boesch-Achermann, 2000). Chimpanzee communities can be defined spatially and behaviorally. Members of the same community range together over geographically circumscribed areas (Nishida & Kawanaka, 1972; Goodall, 1986; Herbinger *et al.*, 2001; Williams *et al.*, 2002), while male chimpanzees are extremely aggressive towards individuals of other communities (Goodall *et al.*, 1979; Wrangham, 1999; Watts & Mitani, 2000, 2001; Muller, 2002; Watts *et al.*, 2002).

Within communities, male chimpanzees are well known for forming strong social bonds. These bonds are manifest between pairs of individuals and are most evident in nonrandom patterns of associations, grooming, and proximity (Nishida, 1968; Simpson, 1973; Goodall, 1986; Goldberg & Wrangham, 1997; Newton-Fisher, 1999; Watts, 2000). Whether social bonds exist at a higher level of organization above dyadic pairs, however, has remained unexplored. To address this problem, we investigated the social behavior and use of space by male chimpanzees living in an unusually large community at Ngogo, Kibale National Park, Uganda. The Ngogo chimpanzees provide an ideal opportunity to examine community social structure and organization. With over 140 members, this community is considerably larger than all others described in the wild (*cf.* Table 21.1 in Wrangham, 2000). Our long-term observations additionally provide a framework to interpret intra-community social relationships between pairs as well as groups

of males (Watts, 2000, 2002; Mitani *et al.*, 2000, 2002; Mitani & Watts, 2001). Our results represent the first evidence for social clustering among wild chimpanzees above the level of dyadic pairs. We investigate some of the behavioral correlates of subgrouping to determine why subgroups form and discuss these findings in the context of the unusual demographic size and structure of the Ngogo community.

Methods

Study site and animals

We observed chimpanzees at the Ngogo study site in Kibale National Park, Uganda. Mitani made behavioral observations during 13 months over 4 years between 1999 and 2002: June-August 1999; May-August 2000; June-August 2001; May-July 2002. Ngogo lies at an interface between lowland and montane rain forest and is covered primarily with moist, evergreen forest. Ghiglieri (1984), Butynski (1990), and Struhsaker (1997) provide detailed descriptions of the Ngogo study area.

The Ngogo community is unusually large and contained approximately 150 individuals with 22-24 adult and 13-15 adolescent males during the 1999-2002 study period. Two adult males and two adolescent males disappeared and presumably died during the four years considered here. In addition, two adolescent males attained adulthood, while another two juvenile males matured and reached adolescence. We limit analyses to the 35 males who were present and in the requisite age categories throughout our observations.

We have worked with the Ngogo chimpanzees since 1995 and do not know the precise age of any of our subjects. To arrive at age estimates, we followed our previous work (Mitani *et al.*, 2002) and classified males into five age categories originally established and defined by Goodall (1968). During the middle of the four-year observation period in 2000, we sorted males into these age categories and assigned them chronological ages at the midpoint of each category, with males in the oldest age class assigned an age of 33.

Behavioral observations

Chimpanzees form temporary parties that vary in size and composition (Nishida, 1968). Following our previous research, we defined parties to include all individuals present and within visual range when we first contacted chimpanzees, typically at the start of the day (Pepper *et al.*, 1999). To ensure statistical independence, we usually recorded parties only once each day. Multiple parties were scored on the same day in cases where they were clearly spatially segregated by hundreds of meters and party membership did not overlap. For each party sighted, we recorded the presence or absence of each adult and adolescent male. The following analyses are based on 511 observations of parties made during the 13 months of study.

We followed target males during hour-long samples to record their grooming behavior and proximity to other chimpanzees. While following targets, we conducted scan samples at 10-minute intervals. During these scans, we noted grooming activity involving targets and scored proximity whenever targets came within 5 meters of other males. Prior analyses indicated that

observations recorded every 30 minutes were statistically independent (Mitani *et al.*, 2000), and we used this interval to score grooming and proximity. Analyses presented below are based on over 2,500 hours of observations with each of the 35 males present throughout the study followed a minimum of 60 hours (mean \pm SD = 72 \pm 9).

Male chimpanzees exhibit aggression between and within communities (Bygott, 1979; Goodall *et al.*, 1979; Muller, 2002). Males are typically hostile to others living in different communities with interactions between them some times resulting in fatalities. Since 1999 we have witnessed male chimpanzees in the Ngogo community kill seven individuals of different groups (Watts & Mitani, 2000; Watts *et al.*, 2002; Watts, Mbabazi & Mitani, unpubl. obs.). Male chimpanzees at Ngogo frequently patrol the boundaries of their territories to seek information about or contact with members of other communities (Watts & Mitani, 2001). We recorded participation in these territorial boundary patrols *ad libitum*. Chimpanzees are also aggressive toward conspecifics in their own social group. Males frequently charge and hit others (Goodall, 1986). We noted such cases of intra-community aggression *ad lib*. To avoid aggression, subordinate chimpanzees give a distinctive call, the pant grunt, to higher-ranking individuals (Bygott, 1979; Hayaki *et al.*, 1989). We recorded these calls as they occurred along with mating activity between males and females.

Statistical analyses

To investigate male subgrouping behavior, we analyzed party compositions using hierarchical cluster analysis. Results of this analysis revealed the existence of two discrete male subgroups. We used these subgroups in matrix correlation tests to examine the relationships between subgroup membership and grooming, proximity, patrol participation, aggression, and maternal genetic relatedness.

Cluster analysis

We performed a hierarchical cluster analysis based on party composition data collected during the entire four years of observation. Clusters were combined with the average linkage between groups method, often called the unweighted pair-group method using arithmetic averages (UPGMA; Sneath & Sokal, 1973). We used the pairwise affinity index (Pepper *et al.*, 1999; Mitani *et al.*, 2002) to construct distance metrics between individuals. Computationally this index is:

$$\frac{I_{AB}}{I_A + I_B}$$

where I_{AB} = the total number of interactions observed between individuals *A* and *B*, I_A = the total number of interactions observed between individual *A* and all other individuals, and I_B = the total number of interactions observed between individual *B* and all others. Interactions here are defined as two individuals appearing together in the same party. The advantage of this index over other association indices is that it factors out each individual's general gregariousness or tendency to interact. Consequently, it reflects only the interaction intensity that is specific to a particular dyad, rather than being generic to one or both individual's behavior (Pepper *et al.*, 1999). We converted these pairwise similarity scores to distances and used squared Euclidean distances to perform the UPGMA cluster analysis. We conducted two additional cluster analyses to investigate the temporal stability of subgroups. For these analyses, we divided our sample in two, using party composition data from 1999-2000 and comparing them with those from 2001-2002.

Matrix correlation tests

We used matrix correlation tests to investigate the relationships between grooming, proximity, and patrol participation and subgroup membership. For these tests we began by constructing 35×35 matrices of pairwise values for subgrouping and each measure of social affinity: grooming; proximity; and joint patrol participation. The subgrouping matrix reflected whether males belonged to the same or different subgroup and contained values of one or zero, respectively.

We employed the pairwise affinity index to construct behavioral matrices. Before using the observed pairwise affinity values, we normalized them by dividing by their expected values under the null hypothesis that social behaviors were generic rather than dyad-specific (*cf.* Mitani *et al.*, 2002). To generate these expected values we used the GROUPS computer program, which implements the group randomization method (Pepper *et al.*, 1999; Mitani *et al.*, 2002). Here 'groups' were defined in terms of one of the three social behaviors we recorded. This procedure repeatedly re-shuffles the membership of observed groups, while retaining both the observed number of appearances of each individual and the observed distribution of group sizes. After each randomization the affinity index was calculated for each dyad, and these randomized values were averaged to generate an expected value for each dyad. We performed 10,000 randomizations to generate null expectations. The randomization procedure simulates a scenario in which individuals may vary in their tendency to interact, but do not discriminate among potential partners. It controls for potentially confounding factors, such as the number and sizes of observed groups and the differing number of appearances of individuals by explicitly incorporating them into the null model. The resulting ratio of observed to expected values indicates the direction and magnitude of each dyad's deviation from generic or indiscriminate behavior.

We used the tau K_r matrix partial correlation procedure (Hemelrijk, 1990a) to test the null hypothesis that male subgroup membership was unrelated to a given social behavior. In these tests, we examined the association between subgroup membership and grooming, proximity, and patrol participation, while controlling for the effect of association. For these tests, we employed a third matrix of association frequencies between dyadic pairs of males based on party compositions. We performed three comparisons, testing subgroup membership against each social behavior. To correct for the increased probability of committing type I error when making these three comparisons, we adjusted our criteria of significance downward using the sequential Bonferroni technique (Holm, 1979). For k multiple tests, we set our adjusted alpha levels, α' , at: $\alpha' = \alpha / (1 + k - i)$, where $\alpha = 0.05$ = the overall experiment-wise error rate and i = the i 'th sequential test from first to last.

We conducted an additional matrix correlation test to investigate the relationship between aggression and subgroup membership after controlling for association frequency. In this test we used the subgroup matrix as described above and aggression and association matrices consisting of frequencies of each between dyadic pairs of males. In a final analysis, we examined whether males in the same subgroup were closely related genetically through the maternal line. Here we utilized the K_r matrix correlation test (Hemelrijk, 1990b) to compare subgroup membership with mtDNA genetic distances. For this comparison, we extended our prior work (Mitani *et al.*, 2000, 2002) by sequencing a 1038 bp region of the mitochondrial D loop. We applied Kimura's (1980) two-parameter model to estimate mtDNA genetic distances between the 35 males, using a transversion to transition ratio of 10 : 1.

Correlates of subgrouping behavior

We employed nonparametric Mann-Whitney U tests to examine whether males in each of the subgroups differed in age, mating activity, and rank. We used a two-tailed Mann-Whitney U test to compare the average age of males in the two subgroups. We tallied the number of copulations achieved by each male and investigated whether the mating success of males in one subgroup was higher than that of individuals in the other subgroup.

We used the distribution of pant grunts to construct a 35×35 dominance matrix and used the MatMan software package (Version 1.0; de Vries *et al.*, 1993) to assign dominance ranks to individuals. MatMan tests the linearity of a dominance hierarchy based on Landau's (1951) index and implements an iterative procedure to rank individuals in a way to minimize the number and strength of inconsistencies between them (de Vries, 1995, 1998). In a third Mann-Whitney test, we compared the dominance ranks of males in the two subgroups.

Spatial analyses

We used a grid-cell analytical method to examine the congruence of range use between males of the different subgroups (Doncaster, 1990). For this analysis, we superimposed a 500×500 meter grid of cells over the study area (Fig. 4). We then plotted the use of these cells by each male in each subgroup. To ensure statistical independence, we recorded only one daily location for each male, scoring the place he was first observed each day for this purpose. We took the resulting range utilization distributions for each subgroup and compared them with a Spearman rank correlation test to investigate their degree of congruence (Doncaster, 1990).

Results

Subgroups and male social behavior

Figure 1 shows the results of the UPGMA cluster analysis using observations of party compositions. Two clear subgroups of males emerged from this analysis. One consisted of 23 males, including 17 adults and 6 adolescents (subgroup A). Another 5 adults and 7 adolescents composed a smaller group (subgroup B).

We used the subgroups defined by the cluster analysis to explore the relationships between subgroup membership and male social behavior. Matrix partial correlation tests revealed that members of the same subgroup tended to remain in proximity and participate in boundary patrols together after holding the effect of association frequency constant (proximity: two-tailed $p = 0.0002$, $\alpha' = 0.0017$; patrols: two-tailed $p = 0.0002$, $\alpha' = 0.025$; Table 1). In contrast, subgroup membership failed to predict the tendency of males to groom with each other after controlling for frequency of association (two-tailed $p = 0.06$, $\alpha' = 0.05$; Table 1).

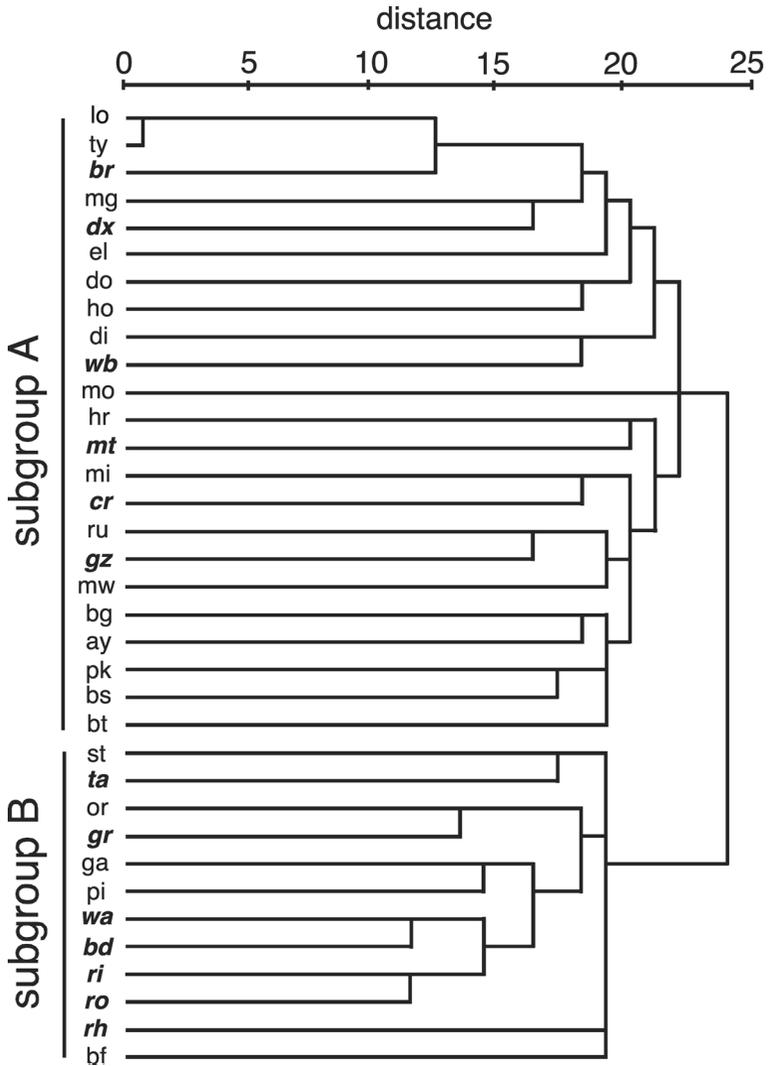


Fig. 1. UPGMA cluster analysis dendrogram of party compositions. Two subgroups of males, A and B, are clearly shown. Plain text = adult males. *Italics* = adolescent males.

Given the extremely large size of the Ngogo community, aggression between males was a regular occurrence. We recorded 1184 acts of aggression between community males. After controlling for how often males associated with each other, aggression occurred significantly more often within than between subgroups (two-tailed $p = 0.0006$; Table 1).

TABLE 1. *Relationships between subgroup membership and grooming, proximity, participation in boundary patrols, and aggression after controlling for association frequency*

	Subgroup membership	
	tau K_r	p
Grooming	0.07	0.06
Proximity	0.17	0.0002
Patrols	0.19	0.0002
Aggression	0.11	0.0006

Tau K_r matrix correlation statistics and associated p values are shown.

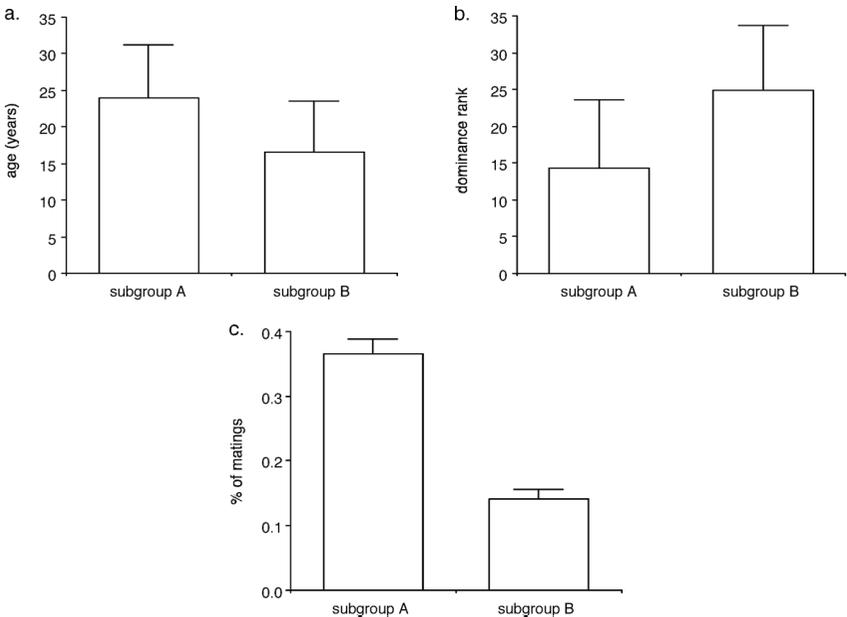


Fig. 2. Correlates of male subgrouping behavior. (a) Male age. (b) Male dominance rank. (c) Male mating success. Means + one SD of males in each subgroup are displayed.

Correlates of subgrouping behavior

Members of the same subgroup were not closely related through the maternal line as assayed by mtDNA genetic distances ($K_r = 755$, two-tailed $p > 0.05$). While maternal kinship did not predict who associated with whom in subgroups, consistent differences in male age, dominance rank, and mating

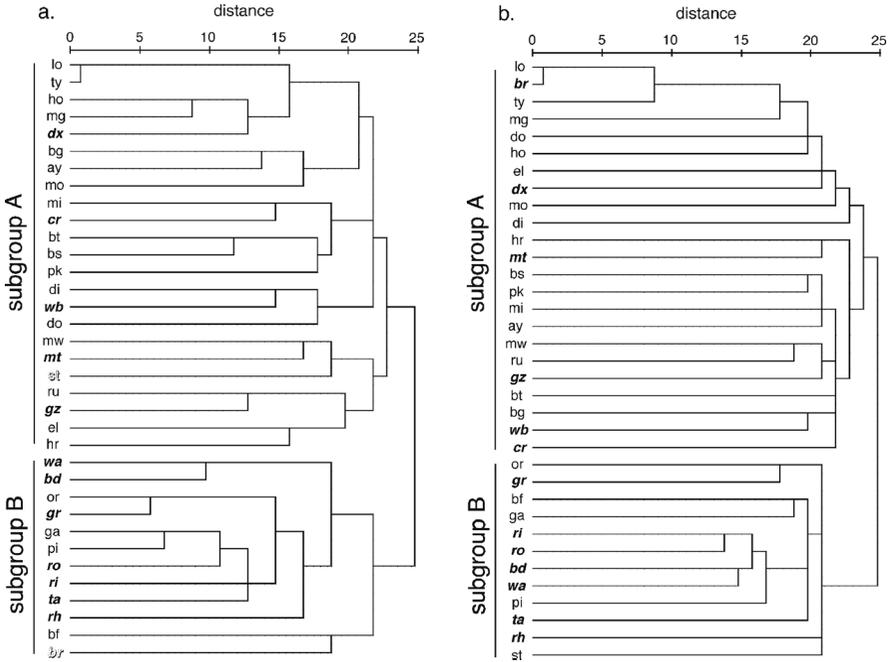


Fig. 3. UPGMA cluster analysis dendrograms of party compositions during 1999-2000 and 2001-2002. Two subgroups of males, A and B, are clearly shown. Males who moved between subgroups during the two periods are shown in outline form. Plain text = adult males. *Italics* = adolescent males.

activity existed between subgroups. The seven adolescent males in subgroup B were among the youngest males in the entire community. Consequently, males in this subgroup were considerably younger than those in subgroup A (Mann-Whitney $U = 66$, $N_1 = 23$, $N_2 = 12$, $p < 0.01$; Fig. 2a). Male age was correlated with dominance rank (Spearman $r = -0.72$, $N = 35$, $p < 0.01$), and males in subgroup B were lower ranking than members of subgroup A (Mann-Whitney $U = 55$, $N_1 = 23$, $N_2 = 12$, $p < 0.01$; Fig. 2b). Consistent with previous reports (Watts, 1998; Watts & Mitani, 2001), there was a significant relationship between male dominance rank and mating success (Spearman $r = 0.78$, $N = 35$, $p < 0.001$). The mating success of males in subgroup B was therefore lower than that of males in subgroup A (Mann-Whitney $U = 53$, $N_1 = 23$, $N_2 = 12$, $p < 0.01$; Fig. 2c).

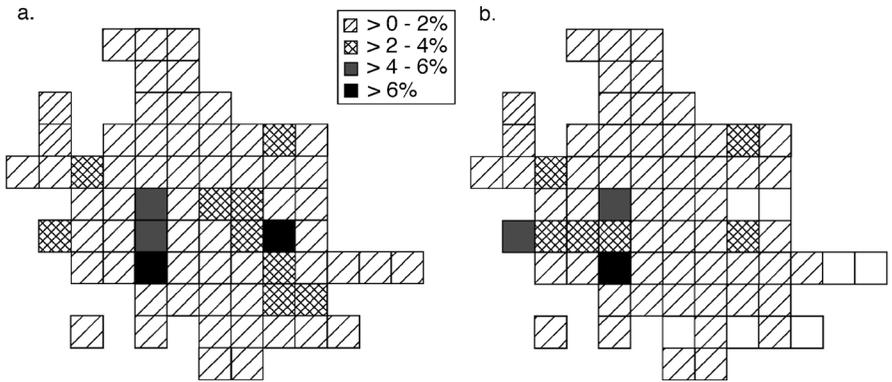


Fig. 4. Range use by male chimpanzee subgroups at Ngogo. (a) Range use by males of subgroup A identified in Fig. 1. (b) Range use by males of subgroup B identified in Fig. 1. Each grid cell represents a 500×500 m area. The percentage of time males of each subgroup spent in each cell is shown.

Temporal stability of subgroups

Figure 3 displays cluster analysis dendrograms based on party compositions recorded during 1999-2000 and 2001-2002. There was remarkable temporal stability in the composition of these subgroups. Two discrete subgroups of 23 and 12 males were apparent during both periods. Only two males differed in their subgroup membership over time. Adult male ST moved from subgroup A to B, while adolescent male BR shifted from subgroup B to A (Fig. 3). The compositions of the two subgroups during the last two years of observation in 2001-2002 did not differ from those displayed over the entire four-year study period (Figs 1 and 3b).

Use of space

Male chimpanzees at Ngogo utilized 70, 500×500 m grid cells covering 17.50 km^2 (Fig. 4). This figure, based on first contact data collected during daily observations of individual males, represents a minimum estimate of the territory size of the Ngogo community. Males in subgroup A used all 70 grid cells, while males in subgroup B ranged over a slightly smaller 15.75 km^2 area. Males in the two subgroups shared use of 63 of the 70 cells or 90% of the total range.

Figure 4 depicts range use by males of each subgroup. There was significant overlap in the use of space by members of the different subgroups; range

utilization distributions of the two were positively correlated with each other (Spearman $r = 0.77$, $N = 71$, two-tailed $p < 0.001$).

Discussion

The results presented here provide the first evidence that wild chimpanzees affiliate above the level of dyadic pairs of individuals. At Ngogo two distinct subgroups of male chimpanzees can be defined on the basis of their associations in temporary parties. Members of the same subgroup maintained proximity to each other and jointly patrolled their territory. Subgroups did not form along the lines of maternal kinship. Instead, predictable differences in male age, dominance rank, and mating success existed between subgroup members. Collectively, males in a smaller subgroup (subgroup B; Fig. 1) were younger, lower ranking, and achieved lower mating success than individuals in a second, larger subgroup (subgroup A; Fig. 1). Despite this social clustering, males in the different subgroups were not overly hostile to each other. In fact, most aggression occurred within rather than between subgroups. Furthermore, subgroup membership did not lead to differences in range utilization, with males in each subgroup showing a significant degree of overlap in their use of the community territory.

Nishida (1968, 1979) and colleagues (Uehara, 1981; Kawanaka, 1984) were the first to clarify the fission-fusion nature of chimpanzee society at the Mahale Mountains, Tanzania. Their studies showed that chimpanzee communities revolve around a core group of adult males, who interact non-randomly with each other. Subsequent research has revealed additional complexity in the social relationships of male chimpanzees. Males frequently engage in temporary coalitions and long-term alliances and cooperate in hunting, meat sharing, and lethal raids on neighboring communities (Nishida, 1983; Nishida *et al.*, 1992; Boesch, 1994; Nishida & Hosaka, 1996; Wrangham, 1999; Mitani & Watts, 2001; Watts & Mitani, 2001; Watts, 2002).

Despite the impressive array of cooperative behavior displayed by male chimpanzees, research to date has failed to show any hierarchical patterning of social interactions above the dyadic pair. The subgroups documented here now indicate that higher order social bonds exist. Why do subgroups form at Ngogo? Our results suggest that subgrouping behavior may represent a normal part of chimpanzee development. As they attempt to integrate

themselves into chimpanzee society, adolescent males frequently seek the company and support of adult males with whom they develop grooming and other social relationships (Hayaki, 1988; Pusey, 1990). This process of social integration is likely to be very difficult in the unusually large Ngogo community. Seen in this context, the integrity of subgroup B may ultimately depend on the behavior of adolescent males. If this hypothesis is correct, then the short-term temporal stability of subgroups documented here (Fig. 3) should give way to changes as adolescent males mature and move into the ranks of adulthood. We plan to test this hypothesis in future work.

To our knowledge, the social patterns that we have described are unique to the Ngogo chimpanzees. Several primates and other mammals display a hierarchical social organization (Moss & Poole, 1983; Stambach, 1987; Bennett & Sebastian, 1988; Connor *et al.*, 1992; Bleisch *et al.*, 1993). For example, one-male units gather in larger clans, bands, herds, and troops in hamadryas and gelada baboons (Stambach, 1987). Social units in these situations, however, are not based on age-graded sets of individuals. Juvenile flocks in birds and bachelor bands in mammals (*e.g.* Heinrich, 1988; Yamagiwa, 1987; Whitehead & Weilgart, 2000) furnish additional analogs to the subgroups of males at Ngogo, but in neither of these cases do individuals gather within a larger, stable community or group. It is presently unclear why these differences exist. Clear costs prohibit male chimpanzees forming bachelor bands outside their social community (Wrangham, 1999). Other factors are likely to operate, and explaining this interspecific variation will require further study.

One persistent question about the Ngogo chimpanzee community concerns its stability. Given the community's unusually large size and the well-known group fissioning events that have been described in chimpanzees (Goodall, 1986), their closely related congener, the bonobo (Kano, 1992), and other primates (Nash, 1976; Melnick & Kidd, 1983; Cords & Rowell, 1986; Struhsaker & Leland, 1988; Windfelder & Lwanga, *in press*), it is reasonable to ask whether this community will split in the near future. Our observations do not provide any hint that the Ngogo community is in the process of doing so despite the social clustering of males documented here. One might hypothesize that increased levels of aggression between males of the different subgroups would serve as a prelude to group fissioning. In contrast to this expectation, however, our data indicate that more aggression occurred within rather than between subgroups. The significant degree of

range overlap between members of the different subgroups also shows that the Ngogo males continue to share the use of a common territory. In sum, the behavioral and spatial integrity of the Ngogo chimpanzee community appears intact. Determining the factors that permit this community to maintain its unusual demographic size and structure remains a central challenge for future research.

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